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Les éléments de l'attractivité féminine et leurs variations

Jeanne Bovet

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THÈSE

Pour obtenir le grade de
Docteur

Délivré par **UNIVERSITE MONTPELLIER 2**

Préparée au sein de l'école doctorale Systèmes Intégrés
en Biologie, Agronomie, Géosciences, Hydrosciences
et Environnement

Et de l'unité de recherche Institut des Sciences de
l'Evolution de Montpellier

Spécialité : **Biologie**

Présentée par **Jeanne BOVET**

**LES ELEMENTS DE L'ATTRACTIVITE
FEMININE ET LEURS VARIATIONS**

Soutenue le 09/12/2014 devant le jury composé de

Mr Michel RAYMOND

Directeur de recherche, ISEM, CNRS, Université de Montpellier

Mme Charlotte FAURIE

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Aux participants, femmes et hommes, de mes études

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I. Introduction

«Je ne puis trop répéter combien j'estime la beauté, qualité puissante et avantageuse. Socrate l'appelait une courte tyrannie, et Platon, le privilège de nature. Nous n'en avons point qui la passe en crédit. Elle tient le premier rang au commerce des hommes ; elle se présente au-devant, séduit et préoccupe notre jugement avec grande autorité et merveilleuse impression.»

Montaigne, Essais, 1588

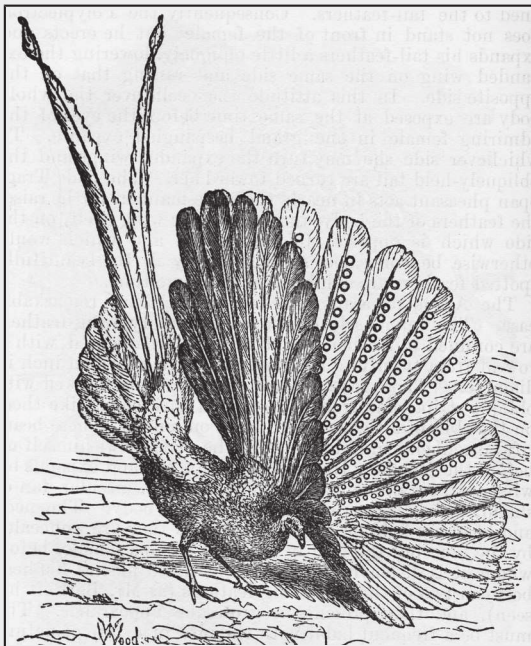
La question de la beauté, qui se retrouve déjà chez les premiers philosophes, a depuis été abordée par de nombreuses disciplines scientifiques. L'attractivité physique a des effets dans de nombreux domaines de la vie, et nous attribuons plus facilement des qualités positives aux personnes attirantes, et des qualités négatives à celles qui le sont moins (Dion, Walster et al. 1972; Eagly, Makhijani et al. 1991). En conséquence, nous avons tendance à agir différemment avec les individus sur la base de leur attractivité physique (Dion 1974; Stewart 1980; Stewart 1985; Langlois, Ritter et al. 1995). Au cours de cette thèse, la beauté sera abordée d'un point de vue évolutionniste, dans le cadre du choix du partenaire, et l'attractivité sera définie comme la capacité à attirer les individus du sexe opposé.

Encadré 1. Le choix du partenaire, un processus majeur de la sélection sexuelle

"Mate choice has been recognized as the most important mechanism through which sexual selection influences evolution" (Andersson 1994).

La sélection sexuelle fait référence aux différences de reproduction entre les individus, qui résultent d'*avantages* reproductifs, indépendants des avantages liés aux différences de survie (Gangestad and Simpson 2000). Traditionnellement, les effets de la sélection sexuelle sont séparés en deux catégories :

- La première concerne la compétition entre les individus du même sexe, pour accéder aux partenaires du sexe opposé. On parle dans ce cas de sélection intrasexuelle, qui conduit à des adaptations de traits phénotypiques représentant des atouts lors d'affrontements entre conspécifiques du même sexe.
- La seconde concerne la capacité à attirer les membres du sexe opposé. On parle alors de sélection intersexuelle, et c'est dans cette catégorie que se situe le choix du partenaire. Il s'agit d'une force évolutive majeure pouvant conduire à l'apparition de caractères sexuels secondaires tels que les ornements, ou de comportements complexes.



Argus géant (*Argusianus argus*) en position de parade devant une femelle.

Dessin de Thomas Waterman Wood
(Darwin 1871)

I.1. Le choix du partenaire, une force évolutive

La qualité en tant que partenaire est variable entre les individus, tout comme les aliments varient en termes de valeur nutritive (Singh 2006). Puisque les partenaires potentiels ne sont pas tous équivalents, le fait de choisir, plutôt que de prendre un partenaire au hasard parmi ses congénères de sexe opposé, peut permettre à un individu de produire plus de descendants (Geary 2004), et un mauvais choix aura manifestement un impact négatif sur le potentiel reproducteur de l'individu. Le choix du partenaire, qui peut être défini comme tout schéma de comportement augmentant la probabilité de s'accoupler avec certains individus plutôt qu'avec d'autres (Halliday 1983), représente donc un avantage évolutif.

i. Les préférences, un mécanisme adaptatif

Les préférences sont des mécanismes psychologiques qui nous poussent à agir d'une façon qui augmente notre valeur sélective, dans les conditions environnementales sous lesquelles elles ont été sélectionnées. Ainsi, manger un fruit mûr apporte des calories et des nutriments vitaux, et s'accoupler avec un conspécifique sexuellement mature du sexe opposé permet de se reproduire. A l'inverse, les aversions empêchent les comportements délétères pour la survie ou la reproduction (par exemple, la peur des serpents réduit les probabilités de se faire mordre). Autrement dit, une préférence est sélectionnée lorsqu'elle augmente la probabilité qu'un individu interagisse avec un stimulus d'une façon qui va augmenter la fréquence des allèles liés à cette préférence (Buss 2005). Dans le cas du choix du partenaire, la sélection va favoriser les mécanismes permettant d'identifier la valeur des différents partenaires potentiels, et va agir sur la propension à être attiré par les individus de haute qualité ou compatibilité.

Encadré 2. Des processus psychologiques inconscients

Il est important de noter que les préférences sont, du moins en partie, des mécanismes inconscients. Un homme, tout comme un chimpanzé ou un rat, peut exprimer une préférence sans avoir conscience des facteurs ayant provoqués cette attirance (Zajonc 2000; Berridge & Winkielman 2003; Berridge 2003). Même dans le cas où un individu se rend compte des facteurs ayant influencé son choix (il peut savoir, par exemple, qu'il préfère les aliments sucrés par rapport aux aliments amers), il ne sera pas pour autant conscient du lien entre le trait préféré et la propriété dont il est l'indice (le sucre représente une source d'énergie pour l'organisme alors que l'amertume est souvent associée à une toxicité (Scott & Mark 1987; Glendinning 1994)).

Le caractère inconscient des préférences va impacter les méthodes d'investigation des chercheurs en comportement. Ainsi, la plupart des études sur le choix du partenaire chez l'humain sont réalisées en demandant aux participants de donner une note d'attractivité, ou de faire un choix parmi plusieurs stimuli («Quelle femme trouvez-vous la plus attirante ?»), et non en posant directement une question du type : «Quels critères utilisez-vous pour choisir une partenaire ?». Cette méthode a également l'avantage de limiter les réponses conformes à un attendu social, ne reflétant pas forcément les préférences réelles d'un individu.

D'autres techniques permettent même de s'affranchir de la verbalisation. Il est ainsi possible de mesurer des réponses physiologiques qui ne sont pas sous le contrôle de la conscience. Par exemple, le diamètre de la pupille est utilisé comme une mesure de l'intérêt et du plaisir que procure un stimulus (Hess & Polt 1960; Laeng & Falkenberg 2007). D'autres études utilisent également l'imagerie par résonance magnétique (IRM) pour analyser l'activité des zones du cerveau pendant la présentation de stimuli (Winston, O'Doherty et al. 2007; Platek & Singh 2010; Holliday, Longe et al. 2011). La conductance de la peau (liée à la transpiration) est également un moyen d'accéder aux réponses inconscientes des individus (Ellis, Young et al. 1993; Ellis, Quayle et al. 1999).

ii. Les préférences des mâles

Darwin remarqua que les caractères sexuels secondaires (plumages ou pelages richement colorés, ornements sophistiqués) sont plus souvent observés chez les mâles, et proposa que, le plus souvent, ce sont les femelles, et non les mâles, qui choisissent leur partenaire (Darwin 1871). Cette différence découle notamment de l'investissement initial dans les gamètes, souvent suivi de soins parentaux, généralement plus importants pour les femelles (Trivers 1972). Cet investissement initial plus grand rend les femelles plus discriminantes. Cependant, il existe un certain nombre d'espèces chez lesquelles les mâles montrent des préférences pour s'accoupler avec certaines femelles plutôt qu'avec d'autres (Dewsbury 1982; Kraaijeveld, Kraaijeveld-Smit et al. 2007). Ainsi, des préférences d'appariement des mâles ont été documentées chez des insectes (Kvarnemo & Simmons 1999; Bonduriansky 2001), des poissons (Sargent, Gross et al. 1986; Berglund & Rosenqvist 2001; Kvarnemo, Moore et al. 2007), des lézards (LeBas & Marshall 2000; Orrell & Jenssen 2002), des oiseaux (Amundsen 2000; Jones, Monaghan et al. 2001; Schamel, Tracy et al. 2004; Torres & Velando 2005; Kraaijeveld, Kraaijeveld-Smit et al. 2007) et des mammifères (Berger 1989; Keddy-Hector 1992; Domb & Pagel 2001; Craig, Herman et al. 2002; Preston, Stevenson et al. 2005; Parga 2006).

Les préférences des mâles sont variées. Dans certaines espèces, les mâles préfèrent des partenaires familières (Huck & Banks 1979), alors que dans d'autres, ils en préfèrent de nouvelles (Orrell & Jenssen 2002). Parfois, les mâles préfèrent des partenaires plus âgées, plus grosses ou plus dominantes (Szykman, Engh et al. 2001; Werner & Lotem 2003; Wong & Jennions 2003; Herdman, Kelly et al. 2004; Preston, Stevenson et al. 2005; Muller, Thompson et al. 2006; Kvarnemo, Moore et al. 2007), alors que dans d'autres

espèces, ils préfèrent des partenaires plus jeunes (Orrell, 2002 #365). Dans les espèces où les femelles sont colorées ou présentent des ornements, les mâles préfèrent généralement les femelles les plus colorées ou les plus richement ornementées (Amundsen 2000; LeBas & Marshall 2000; Berglund & Rosenqvist 2001; Domb & Pagel 2001; Griggio, Valera et al. 2005; Torres & Velando 2005). Les préférences des mâles leur permettent d'augmenter leur succès reproducteur, puisque les caractéristiques qu'ils préfèrent chez les femelles sont généralement corrélées à des différences en termes de fécondité et/ou de qualité d'investissement maternel (McLennan 1995; Berglund, Rosenqvist et al. 1997; Jones, Monaghan et al. 2001; Szykman, Engh et al. 2001).

Dans l'espèce humaine, les deux sexes expriment des préférences en termes de choix du partenaire, même si le poids du choix de chaque sexe dans la formation d'un couple n'a jamais été quantifié. La valeur en tant que partenaire chez l'humain comprend des qualités phénotypiques comme la santé, la fécondité, l'âge, l'intelligence, le statut social, les compétences parentales, ou la volonté et la capacité à investir dans les descendants (Buss 1989; Symons 1995; Thornhill & Gangestad 1999; Buss 2005). De plus, comme une partie de la variance de la qualité phénotypique est héritable, certains aspects phénotypiques reflètent une qualité génotypique sous-jacente. La psychologie humaine doit permettre (consciemment ou inconsciemment) d'évaluer un partenaire potentiel à partir d'indices associés à chacune de ces composantes, de pondérer leur importance relative en fonction des conditions présentes, puis d'assimiler ces données pour parvenir à une estimation pratique de la valeur du partenaire (Symons 1995; Buss 2005). Certains indices de la qualité du partenaire sont physiquement observables, et la somme de leur évaluation contribue à notre perception de l'attractivité physique de l'individu. Certains traits associés à une haute qualité en tant que partenaire chez un homme diffèrent de ceux associés à une

haute qualité de partenaire pour une femme. Dans ce cas, les critères de l'attractivité féminine et masculine vont être différents.

I.2. Le choix d'une partenaire fertile

De manière générale, les hommes accordent plus d'importance que les femmes à l'attractivité physique d'une partenaire, car le potentiel reproductif d'une femme est étroitement liée à sa condition physiologique (Buss 1989) : puisque le succès reproducteur d'un homme est en grande partie déterminé par la fertilité de la (ou des) partenaire(s) qu'il choisit, les mécanismes psychologiques permettant aux hommes de détecter les indices de fertilité d'une femme vont être sélectionnés, et l'intensité de l'attraction sexuelle des hommes va varier en fonction de ces indices (Symons 1995). Nous définirons ici la fertilité féminine comme la capacité à produire des descendants viables, comprenant la probabilité d'une grossesse après un accouplement, la capacité à mener à terme une grossesse engendrant un enfant en bonne santé, et à apporter un allaitement pendant les premiers temps de la vie du nouveau-né.

i. L'âge

L'âge est un des premiers facteurs influençant la fertilité. La fertilité d'une femme augmente rapidement à partir de la puberté, culmine autour de 25 ans en moyenne, puis décline progressivement jusqu'à s'annuler à la ménopause (Symons 1995). Les données concernant les sociétés de chasseurs-cueilleurs rapportent que le pic de fertilité a lieu au début de la vingtaine chez les femmes Yanomamö du Venezuela et chez les !Kung du Botswana, et plutôt à la fin de la vingtaine chez les Aché du Paraguay (Hill & Hurtado

1996). Après 30 ans, la probabilité d'une grossesse diminue, et les risques de fausses-couches et de complications, ainsi que la mortalité (de la mère et de l'enfant) augmentent significativement (Xiaoli & Weiyuan 2014). D'autre part, nous sommes capables d'estimer de façon assez précise l'âge de nos conspécifiques (Rhodes 2009), et il s'agit d'un facteur important dans le choix d'une partenaire. Une étude de Buss (Buss 1989) a montré que, dans 37 cultures, les hommes préfèrent une épouse plus jeune qu'eux-mêmes. Les schémas de mariage dans ces cultures indiquent que cette préférence est mise en pratique : les épouses ont, en moyenne, 3 ans de moins que leur époux. De plus, la différence d'âge préférée par les hommes augmente avec leur propre âge. Autrement dit, quel que soit leur âge, les hommes sont attirés par les femmes ayant un âge proche du maximum de fertilité (Buunk, Dijkstra et al. 2001). Plusieurs études ont montré que des indices du vieillissement se trouvent dans le visage, et que les hommes les utilisent pour juger l'attractivité d'une femme. Il existe en effet un lien étroit entre l'âge perçu et l'attractivité d'un visage (Kwart, Foulsham et al. 2012). D'une part, les traits du visage liés à la jeunesse augmentent l'attractivité des visages de femmes (Jones & Hill 1993; Furnham, Mistry et al. 2004). D'autre part, l'estimation de l'âge et le jugement de l'attractivité d'un visage féminin se font tous deux en partie grâce à la texture de la peau (Samson, Fink et al. 2010). Enfin, la diminution de l'attractivité d'un visage avec l'âge est plus forte pour les femmes que pour les hommes (Maestripieri, Klimczuk et al. 2014).

ii. La santé

Évidemment, l'état de santé d'un individu va affecter sa qualité en tant que partenaire. Premièrement parce-qu'il est dangereux de s'accoupler avec une personne porteuse d'une maladie contagieuse (Tybur & Gangestad 2011), mais aussi parce que l'état de santé d'une

femme peut affecter sa fertilité. De nombreuses pathologies ont un effet délétère sur la capacité à tomber enceinte, le déroulement de la grossesse, ou la santé du descendant. Et puisque l'état de santé d'un individu est en partie déductible de certaines de ses caractéristiques physiques, il va impacter son attractivité.

Prenons le cas de la corpulence, souvent mesuré par l'indice de masse corporel (BMI : Body-Mass Index, correspondant au poids divisé par le carré de la taille). Un poids trop faible ou trop élevé impacte négativement la capacité d'une femme à concevoir (Zaadstra 1993). En effet une femme, si elle est trop maigre (par manque de nourriture ou à cause d'une maladie), cessera d'ovuler ou ne possédera pas assez de ressources pour mener à bien une grossesse, ou un allaitement (Frisch & McArthur 1974; Frisch 1987). A l'inverse, un poids trop élevé (obésité), est lié à des dérèglements du cycle ovarien et à un plus grand risque de fausses couches (Rogers & Mitchell 1952; Hamilton-Fairley, Kiddy et al. 1992; Clark, Thornley et al. 1998). Parallèlement, le BMI semble être l'un des principaux facteurs de l'attractivité d'un corps féminin. Ceci a été montré par des études de préférences utilisant des dessins de femmes de différentes corpulences (Singh 1993; Singh & Young 1995; Swami, Caprario et al. 2006), des images de corps de femmes réalisées par absorption biphotonique à rayons X (Faries & Bartholomew 2012), ainsi qu'un logiciel informatique permettant de créer le corps d'une partenaire idéale en trois dimensions (Crossley, Cornelissen et al. 2012). L'utilisation de la technique de l'eye-tracking (permettant d'enregistrer le mouvement des yeux des observateurs), a mis en évidence un même schéma d'observation lors du jugement de la corpulence et de l'attractivité d'un corps féminin (Cornelissen, Hancock et al. 2009). Enfin, une étude a montré que le BMI et l'historique des antécédents médicaux d'une femme étaient de bons prédicteurs de son attractivité faciale (Hume & Montgomerie 2001).

La qualité de la peau procure non seulement une indication de l'âge (Symons 1995), mais est aussi un témoin de la santé actuelle et passée d'un individu. Il existe en effet un lien direct entre maladies ou infections et lésions ou cicatrices de la peau (Buss 2005). Chez les femmes, certains problèmes de peaux peuvent aussi être corrélés à des troubles hormonaux (Schiavone, Rietschel et al. 1983). Le teint de la peau est lui aussi relié à des facteurs de santé. En effet, la quantité de rouge dans le teint est corrélée à la vascularisation de la peau, qui est positivement reliée à la condition physique (Johnson 1998) et au taux d'œstrogènes chez les femmes (Charkoudian, Stephens et al. 1999; Thornton 2002), mais négativement lié au diabète de type 2 (Charkoudian 2003) et à l'hypertension (Panza, Quyyumi et al. 1990). De plus, l'augmentation de l'oxygénation sanguine rend le sang plus rouge, alors que la désoxygénation du sang, qui est associée aux maladies cardiaques et respiratoires, donne à la peau un teint terne et bleuté (Stephen, Smith et al. 2009). La quantité de jaune est reliée aux caroténoïdes de la peau, provenant principalement de la consommation de fruits et légumes (Alaluf, Heinrich et al. 2002). La complémentation alimentaire en caroténoïdes est associée à une amélioration du système immunitaire (Alexander, Newmark et al. 1985), tandis que les personnes atteintes du VIH ont des taux réduits de caroténoïdes (Friis, Gomo et al. 2001). De plus, les femmes qui ne parviennent pas à concevoir lors de fertilisations in vitro ont des taux de caroténoïdes dans le fluide folliculaire variant de manière inhabituelle (Schweigert, Steinhagen et al. 2003). Plusieurs études ont montré l'importance de la couleur de la peau à la fois pour la santé apparente et l'attractivité des visages. Ainsi, une étude de Stephen & Smith (Stephen, Smith et al. 2009) montre que l'augmentation du rouge, du jaune et de la luminosité sur des photographies de visage de Caucasiens augmente la santé perçue des visages. Une coloration homogène de la peau est corrélée avec les estimations de santé, de jeunesse et d'attractivité des visages (Fink, Grammer et al. 2001; Fink, Grammer et al. 2006; Matts, Fink et al. 2007). Enfin,

Encadré 3. La symétrie du visage

Les caractéristiques physiques externes de beaucoup d'animaux sont censées être bilatéralement symétriques. Cependant, certains événements peuvent perturber le déroulement du développement. De fait, la symétrie est liée à la capacité à résister aux pathogènes, aux anomalies génétiques et au stress développemental, grâce à une utilisation efficace des ressources pendant le développement et/ou grâce à un bon système immunitaire. Maintenir un développement symétrique étant coûteux, la symétrie serait un indice de la qualité génétique et phénotypique d'un individu (Moller 1999; Buss 2005).

La symétrie est censée avoir un effet particulièrement fort sur l'attractivité masculine. En effet, la testostérone ayant un effet immunodépresseur, seuls les mâles possédant une bonne qualité génétique et un bon système immunitaire pourront avoir à la fois un haut taux de testostérone et un haut degré de symétrie (Thornhill & Gangestad 1999; Buss 2005).

Comme attendu, la symétrie est un facteur important de l'attractivité d'un visage. Une préférence pour des visages symétriques a été mise en évidence pour les deux sexes dans de nombreuses études (Grammer & Thornhill 1994; Langlois, Roggman et al. 1994; Rhodes, Proffitt et al. 1998; Mealey, Bridgstock et al. 1999; Perrett, Burt et al. 1999; Rikowski & Grammer 1999; Scheib 1999; Hume & Montgomerie 2001; Penton-Voak, Jones et al. 2001).

La symétrie ne sera pas directement étudiée au cours de cette thèse, mais sera toujours contrôlée, statistiquement ou expérimentalement, durant les tests d'attractivité.

l'âge et les grossesses modifient la couleur de la peau (de Rigal, Des Mazis et al. 2010). Or, la parité est un facteur important de la valeur d'une partenaire car, pour chaque naissance, une femme (dans une population de chasseurs-cueilleurs) perd en moyenne un sixième de sa valeur reproductive résiduelle (correspondant au nombre d'enfants potentiels qu'une femme pourra avoir dans le futur) (Buss 2005).

D'une façon plus générale, les jugements d'attractivité physique (visage ou corps) sont corrélés aux jugements de santé : les personnes attirantes sont jugées en meilleure santé que les personnes ayant une attractivité moindre (Cunningham 1986; Singh 1993; Grammer & Thornhill 1994; Kalick, Zebrowitz et al. 1998). De plus, quelques études ont montré que l'attractivité physique était effectivement reliée à différents indices de santé ((Shackelford & Larsen 1999; Henderson & Anglin 2003) mais voir (Kalick, Zebrowitz et al. 1998) pour un contre-exemple).

iii. Le rôle des hormones

Parmi les femmes en âge de se reproduire et en bonne santé, il subsiste des variations individuelles en termes de fertilité, et les hormones sexuelles y contribuent beaucoup. A la puberté, le taux d'hormones sexuelles dans le sang augmente, et le visage des hommes et des femmes se différencie : chez les garçons, la testostérone stimule la croissance de la mâchoire, des pommettes et des arcades sourcilières, alors que chez les jeunes filles, les œstrogènes inhibent le développement de ces mêmes traits. Ces traits sexuellement dimorphiques signalent donc la maturité sexuelle et le potentiel reproducteur (Johnston & Franklin 1993; Thornhill & Gangestad 1996; Law-Smith, Perrett et al. 2006), et influencent l'attractivité des visages (pour une revue complète voir (Rhodes 2006)). Les études montrant que la féminité augmente l'attractivité utilisent des visages dont le degré de

féminité est mesuré sur photos (Cunningham 1986; Jones & Hill 1993; Cunningham, Roberts et al. 1995; Koehler, Simmons et al. 2004; Komori, Kawamura et al. 2009), ou des visages de femmes modifiés afin d'augmenter ou de diminuer leur féminité (Perrett, Lee et al. 1998; Rhodes, Hickford et al. 2000). De plus, les composites de visages de femmes attractives ont des traits plus féminins, et sont préférés par rapport aux composites moyens (Perrett, May et al. 1994). Enfin, lorsque les participants génèrent eux-mêmes sur ordinateur des visages de femmes attirantes, il créent des visages aux caractères plus féminisés que la moyenne (Johnston & Franklin 1993).

Les œstrogènes ont également comme effet de diriger le stockage des graisses vers les hanches, alors que la testostérone va entraîner un stockage graisseux au niveau de la taille (Bjorntorp 1991; Singh 1993). Le ratio taille/hanche (Waist-to-Hip Ratio : WHR) est donc un bon indicateur du taux d'hormones féminines et de la fertilité d'une femme (Jasienska, Ziolkiewicz et al. 2004). De fait, le WHR d'une femme diminue pendant la puberté, puis augmente généralement après la ménopause. Les femmes avec un faible WHR ont moins de problèmes cardiovasculaires (Spies, Farzaneh-Far et al. 2009), moins de cycles menstruels irréguliers (van Hooff, Voorhorst et al. 2000), ovulent plus fréquemment (Moran, Hernandez et al. 1999), et ont un pH endocervical plus faible, ce qui favorise la pénétration des spermatozoïdes (Jenkins, Brook et al. 1995). Les jeunes filles avec un faible WHR présentent également des taux plus élevés d'œstrogènes au début de la puberté (Deridder, Bruning et al. 1990). De plus, le WHR est directement lié à la capacité à concevoir chez les femmes ayant recours à l'insémination artificielle ou à la fécondation in vitro (Zaadstra 1993; Wass, Waldenstrom et al. 1997). Enfin, le WHR est un marqueur honnête indiquant si une femme est enceinte ou non, et va augmenter avec le nombre de grossesses (Furnham, Lavancy et al. 2001; Sohn & Bye 2012). Par ailleurs, les hommes

Encadré 4. Les seins, un autre indice de fertilité chez la femme ?

Dans l'espèce humaine, la poitrine est un trait sexuellement dimorphique, et les seins des femmes sont de taille importante par rapport à ceux des femelles de primates les plus proches. La morphologie des seins donne des indices sur l'âge, la parité, et l'état de grossesse d'une femme (Symons 1980) : des seins fermes et hauts sont associés à la nubilité, des seins pleins indiquent un allaitement, le degré «d'affaissement» augmente avec l'âge et le nombre de grossesses, et le degré de symétrie de la poitrine est positivement relié à la fertilité (Moller, Soler et al. 1995; Manning, Scutt et al. 1997).

La taille des seins ne semble pas directement reliée à la fertilité ou à l'allaitement (Moller, Soler et al. 1995; Manning, Scutt et al. 1997), bien qu'une étude récente ait trouvé une corrélation positive entre la taille de la poitrine et le taux d'hormones féminines (Jasienska, Ziolkiewicz et al. 2004). Une des hypothèses pouvant expliquer la taille plus ou moins importante de la poitrine des femmes concerne la fertilité résiduelle. En effet, une poitrine importante manifeste plus clairement les changements liés à l'âge ou à la parité. De plus, toutes choses égales par ailleurs, l'asymétrie augmente avec le volume de la poitrine (Manning, Scutt et al. 1997). Des seins de taille importante pourraient être un signal coûteux, donc honnête, de la qualité phénotypique d'une femme et de sa fertilité résiduelle (Moller, Soler et al. 1995; Marlowe 1998).

Cependant, les préférences des hommes pour les différentes caractéristiques de la poitrine féminine sont encore mal connues. Une étude de Singh confirme le lien entre symétrie de la poitrine et attractivité (Singh 1995), mais selon les études et les stimuli utilisés, on observe une préférence pour des seins de taille moyenne à importante (Thompson & Tantleff 1992; Singh & Young 1995; Dixson, Grimshaw et al. 2011), pour des seins de petite taille (Furnham & Swami 2007), ou encore une absence de tendance claire (Furnham, Dias et al. 1998; Furnham, Swami et al. 2006; Swami, Jones et al. 2009; Dixson, Grimshaw et al. 2011).

Comme pour le visage, l'attractivité de la poitrine féminine comprend vraisemblablement plusieurs dimensions, plus ou moins inter-dépendantes, qui correspondent à différents composants de la qualité d'une partenaire.

estiment que les femmes avec un faible ratio taille/hanche (autour de 0,7) sont plus attirantes que les femmes ayant un ratio plus élevé (voir (Singh & Singh 2011) pour une revue complète). Cette préférence a été mise en évidence par des études utilisant des dessins de silhouettes féminines (Singh 1993; Henss 1995; Buunk & Dijkstra 2005), des photos manipulées (Henss 2000; Dixson, Grimshaw et al. 2009; Dixson, Grimshaw et al. 2010), des photos de femmes avant et après avoir eu recours à la chirurgie esthétique (Singh & Randall 2007; Platek & Singh 2010), et un logiciel informatique permettant aux participants de créer le corps de leur partenaire idéale (Crossley, Cornelissen et al. 2012). Enfin, une étude a mis en évidence que les femmes avec un faible WHR avaient leur premier rapport sexuel plus tôt, plus de partenaires sexuels, plus de rapports hors couple, et plus de rapports avec des hommes ayant une autre relation que les femmes avec un WHR plus élevé (Hughes & Gallup 2003). Cependant, d'autres études soulignent l'interdépendance entre WHR et corpulence, ainsi que la difficulté à séparer ces deux composantes (notamment dans la création de stimuli visuels), et mettent en question la part de la variance expliquée par le WHR dans l'attractivité (Tassinary & Hansen 1998; Wilson, Tripp et al. 2005; Swami, Caprario et al. 2006; Holliday, Longe et al. 2011).

Les hormones sexuelles ont également des effets sur la voix. La hauteur de la voix est la caractéristique perçue correspondant à la fréquence fondamentale (F_0), produite par la vibration des cordes vocales. A la puberté, chez les femmes, les œstrogènes et la progestérone produisent les caractéristiques de la voix féminine, d'une fréquence fondamentale d'un tiers inférieure à celle d'un enfant. Chez les hommes, les androgènes vont interagir avec les hormones de croissance et développer des cordes vocales plus larges, plus longues et plus épaisses, propriétés responsables de la fréquence vocale masculine, d'une octave plus basse que celle d'un enfant (Titze 1989). De plus, après une

injection de testostérone, la voix d'une femme va développer des caractéristiques masculines. A l'inverse, les castrats de sexe masculin avaient des voix féminines car les changements physiologiques associés à la testostérone n'avaient alors pas lieu (Abitbol, Abitbol et al. 1999). Enfin, les femmes avec une voix féminine (F0 élevée) ont un taux d'œstrogène plus élevé que les femmes ayant des voix plus masculines (Abitbol, Abitbol et al. 1999). La voix, et en particulier la fréquence fondamentale (F0), serait donc elle aussi un indicateur de l'état hormonal, et donc de la fertilité, d'une femme. Et, comme attendu, les hommes préfèrent les voix plus féminines (d'une F0 plus élevée) (Collins & Missing 2003; Feinberg, DeBruine et al. 2008; Jones, Feinberg et al. 2008). D'autre part, les femmes avec une F0 plus haute ont également un visage plus attirant (Collins & Missing 2003; Feinberg, Jones et al. 2005), ce qui suggère que la voix comme le visage signalent le taux d'hormones féminines, et que les hommes préfèrent à la fois les visages et les voix contenant des indices de forts taux d'œstrogènes.

Il est également intéressant de noter que l'attractivité d'une femme varie au cours de son cycle menstruel. Les changements hormonaux du cycle ovarien induisent des changements au niveau du visage (Roberts, Havlicek et al. 2004), de l'odeur (Singh & Bronstad 2001), et de la voix (Pipitone & Gallup 2008; Bryant & Haselton 2009), auxquels les hommes sont sensibles. Sur la base de ces différents indices, les hommes jugent les femmes plus attirantes au moment où elles sont le plus fertiles (Singh & Bronstad 2001; Roberts, Havlicek et al. 2004; Pipitone & Gallup 2008; Puts, Bailey et al. 2013). Ces changements d'attractivité ne sont pas observés chez les femmes sous contraceptif hormonal (Alvergne & Lummaa 2009).

I.3. Un choix universel ?

Darwin remarqua que certains critères de beauté variaient fortement entre les cultures '*It is certainly not true that there is in the mind of man any universal standards of beauty with respect to the human body*' (Darwin 1871, cité dans Little, Jones et al. 2011). Depuis, la question de l'existence d'une beauté universelle a été explorée par de nombreuses études, notamment dans le domaine de la psychologie évolutionniste. Les préférences en termes de choix du partenaire sont-elles le résultat d'une adaptation commune à tous les groupes humains, ou dépendent-elles des conditions écologiques et culturelles de chaque population ? Le débat est d'importance, car certains psychologues évolutionnistes voient l'universalité des préférences comme une preuve que les critères de beauté ne sont non pas arbitraires et culturellement imposés, mais bien un résultat biologique de la sélection.

i. Variations géographiques

Nous avons vu plus haut que la préférence des hommes envers les femmes jeunes (à l'âge du pic de fertilité) se retrouvait dans de nombreuses populations (Buss 1989). Il existe également un fort consensus inter-culturel pour les jugements d'attractivité des visages (Jones & Hill 1993; Cunningham, Roberts et al. 1995; Jones, Brace et al. 1995; Langlois, Kalakanis et al. 2000; Rhodes, Yoshikawa et al. 2001; Cunningham, Barbee et al. 2002; Dion 2002). Ces résultats suggèrent l'existence de préférences universelles, et contredisent l'idée d'une beauté subjective ou culturellement déterminée. Cette hypothèse est renforcée par le fait que les très jeunes enfants (non encore influencés par les standards culturels), préfèrent regarder les visages jugés attirants par les adultes (Kramer, Zebrowitz et al. 1995; Slater, Von der Schulenburg et al. 1998; Rubenstein, Kalakanis et al. 1999), et ce, que les

visages soient d'origine asiatique, africaine ou caucasienne (Langlois, Ritter et al. 1991). Cependant, l'analyse interculturelle des préférences pour la forme du corps féminin donne des résultats plus mitigés.

En effet, plusieurs études ont montré que la corpulence préférée par les hommes chez une femme diffère entre les populations. Aux États-Unis (Singh 1993; Singh 1993; Singh 1994; Rilling, Kaufman et al. 2009), en Pologne (Koscinski 2013) ou encore à Hong Kong (Fan, Liu et al. 2004), les hommes préfèrent des femmes assez minces, mais d'autres études réalisées en Afrique (Furnham & Baguma 1994; Wetsman & Marlowe 1999; Furnham, Moutafi et al. 2002; Tovee, Swami et al. 2006), en Amazonie (Yu & Shepard Jr. 1998; Sugiyama 2004), et dans le Pacifique (Swami, Knight et al. 2007) semblent indiquer une préférence pour des femmes avec un BMI plus élevé. Les variations des préférences pour la corpulence sont vraisemblablement liées à des variables de l'environnement local, tel que le climat ou le niveau de ressources. Puisque la graisse représente une réserve de calories, une corpulence relativement élevée est un avantage dans les milieux où les quantités de nourriture sont imprévisibles. La seconde fonction biologique de la graisse étant l'isolation thermique, il est également avantageux d'avoir -et de préférer- une corpulence importante dans les milieux froids. Puisque la quantité de nourriture et le climat sont écologiquement variables, il est logique que les adaptations psychologiques liées aux jugements d'attractivité ajustent le niveau des préférences pour la corpulence en fonction de ces critères (Sugiyama 2004). Et effectivement, plusieurs études montrent que la corpulence idéale varie en fonction de la disponibilité des ressources, et que les hommes ayant accès à moins de ressources (nourriture ou argent) préfèrent des femmes plus corpulentes (Brown & Konner 1987; Sobal & Stunkard 1989; Anderson, Crawford et al. 1992). Dans certaines sociétés actuelles, les ressources alimentaires sont facilement

accessibles et moins sujettes à variation. Avoir une corpulence importante n'est alors plus nécessaire, et la préférence pour un BMI élevé n'apporte alors plus d'avantage. De plus, les problèmes liés au surpoids et à l'obésité - vraisemblablement peu fréquents dans les populations traditionnelles – ont augmenté. La minceur n'est plus forcément liée à un manque de ressources, puisque le BMI est aujourd'hui négativement corrélé au statut social dans plusieurs sociétés (Sobal & Stunkard 1989; Molarius, Seidell et al. 2000; Ball & Crawford 2005). Dans ce contexte, une préférence pour des femmes plutôt minces peut donc s'avérer adaptatif (Anderson, Crawford et al. 1992).

Les variations des préférences concernant le WHR sont moins grandes, ou moins évidentes. Ainsi, une préférence pour un faible WHR a été trouvée dans de nombreux pays (en plus des études citées plus haut qui ont majoritairement été réalisées aux États-Unis) : en Angleterre (Furnham, Tan et al. 1997), en Allemagne (Henss 2000), en Pologne (Rozmus-Wrzesinska & Pawlowski 2005), en Australie (Connolly, Slaughter et al. 2004), en Indonésie (Singh & Luis 1995; Singh 2004; Singh, Dixson et al. 2010), en Chine (Dixson, Dixson et al. 2007), en Nouvelle Guinée (Dixson, Sagata et al. 2010; Sorokowski & Sorokowska 2012), en Afrique du Sud (Swami, Jones et al. 2009), au Cameroun, en Polynésie, et en Nouvelle Zélande (Singh, Dixson et al. 2010). Quelques études ont cependant montré une préférence pour des WHR plus élevés dans des sociétés traditionnelles et isolées, comme en Amazonie (Yu & Shepard Jr. 1998) et en Tanzanie (Marlowe & Wetsman 2001), bien que pour ces deux régions des préférences envers un faible WHR aient été observées dans des études ultérieures utilisant des stimuli différents (Sugiyama 2004; Marlowe, Apicella et al. 2005). Il n'est pas exclu que ces légères divergences soient dues aux stimuli utilisés, qui ont un impact non négligeable sur les résultats (Swami, Jones et al. 2009), et qui ne sont pas toujours adaptés à la population

concernée (silhouettes de femmes Caucasiennes pour la majorité des études), ainsi qu'à la difficulté de dissocier le WHR du BMI. La plus grande constance des préférences concernant le WHR par rapport au BMI peut être due au fait que la distribution corporelle de la graisse (WHR) est un trait sous contrôle majoritairement physiologique, alors que la quantité globale de graisse (BMI) est en grande partie déterminée par des facteurs environnementaux. Le lien physiologique entre fertilité et WHR serait équivalent dans toutes les populations humaines, alors que le lien entre fertilité et BMI serait plus dépendant des conditions environnementales, et donc plus sujet à variations.

Les préférences pour les voix féminines ont également été étudiées de manière interculturelle, même si le nombre de populations étudiées est encore faible à ce jour. En Angleterre et au Canada, une préférence consensuelle a été trouvée chez les hommes pour des voix de femme plus aiguës que la moyenne (Collins & Missing 2003; Feinberg, DeBruine et al. 2008; Jones, Feinberg et al. 2008). Cette préférence pour des voix féminines comparées à des voix plus graves a été retrouvée chez les chasseurs-cueilleurs Hadza en Tanzanie (Apicella & Feinberg 2009).

ii. Variations temporelles

S'il est relativement aisé d'étudier les préférences masculines dans des zones géographiques différentes, il est plus compliqué d'analyser l'évolution de ces préférences dans le temps. Les tests d'attractivité ne pouvant pas être réalisés dans ce cas, seules des preuves indirectes sont disponibles concernant les préférences passées. La représentation des femmes dans les médias est un moyen d'étudier l'évolution des critères d'attractivité au cours du temps. Plusieurs études ont donc analysé les mensurations de femmes ayant été élues pour leur attirance physique lors de concours de beauté (*Miss America, Miss Korea,*

Miss France), ou ayant été choisie comme modèles pour des magazines à large audience masculine (*Playboy*). Ces femmes sont considérées comme représentant les canons de beauté féminins d'une époque donnée.

Garner (Garner, Garfinkel et al. 1980) fut le premier à analyser ce type de données. Il mit en évidence un amincissement graduel, entre 1960 et 1978, des femmes ayant posé pour *Playboy* et des lauréates de *Miss America*. Tout comme Garner, Mazur (Mazur 1986) souligna la variation des critères de beauté au cours du temps. A partir des données de *Miss America* et de *Playboy* entre 1923 et 1990, Singh (Singh 1993) ajouta que, si la corpulence générale de ces femmes diminuaient effectivement durant cette période, leur WHR restait relativement constant (entre 0,68 et 0,72). Ce résultat sera cependant contesté par Freese (Freese & Meland 2002), qui observa un changement significatif du WHR sur la période 1921-2001. Pettijohn (Pettijohn & Jungeberg 2004) a ensuite montré que non seulement le BMI et le WHR, mais aussi la taille des yeux avaient varié sur la période 1960-2000 chez les modèles de *Playboy*. Une étude de 2005 avance que le corps idéal féminin est passé d'une forme plutôt tubulaire (WHR élevé) au début du 20^{ème} siècle à une forme de type « sablier » (faible WHR) au milieu du siècle, avant de retourner vers une forme plus tubulaire à la fin du siècle (Byrd-Bredbenner, Murray et al. 2005). Cette dernière tendance (augmentation du WHR depuis le milieu du 20^{ème} siècle) se retrouve également chez les lauréates de *Miss Korea* (Hong, Park et al. 2009).

iii. Variations inter-individuelles

Même si l'on observe, au sein d'une population et à une époque donnée, un consensus général sur quelle femme est attirante et laquelle ne l'est pas (Langlois, Kalakanis et al. 2000), il existe aussi des variations individuelles des préférences pour certains traits.

Un résultat connu illustrant cette variation entre individus d'une même population concerne la préférence olfactive. Plusieurs études ont montré que les hommes (et les femmes) préfèrent l'odeur d'individus génétiquement dissimilaires pour le complexe majeur d'histocompatibilité (CMH), un groupe de gènes important du système immunitaire (Wedekind, Seebeck et al. 1995; Wedekind & Furi 1997; Thornhill, Gangestad et al. 2003). Contrairement aux traits phénotypiques abordés précédemment, dans ce cas les hommes ne s'accordent pas sur l'odeur la plus attirante, et leurs préférences sont directement liées à leur propre génotype. Puisque l'hétérozygotie des gènes du CMH confère aux descendants une meilleure résistance aux maladies, et que les femmes dont le partenaire porte un CMH similaire ont plus de risques de faire une fausse-couche (Komlos, Zamir et al. 1977), une préférence pour un partenaire ayant un CMH dissimilaire semble être adaptatif.

Pour d'autres traits phénotypiques, c'est choisir un partenaire similaire qui peut augmenter la valeur sélective. On parle dans ce cas d'homogamie. Ce phénomène peut être expliqué de manière générale par une extension de la sélection de parentèle, en posant que les individus peuvent optimiser la transmission de ses gènes en s'appariant avec des individus ayant des gènes en commun (Thiessen & Gregg 1980). Dans une population panmictique, un enfant partage en moyenne 50% de ses gènes avec ses parents. Une homogamie entre les parents va créer un «bonus génétique» de partage supplémentaire. Cela va avoir pour résultat un gain en termes de duplication des gènes, sans augmentation de l'effort reproducteur. Évidemment, la limite de l'homogamie est la dépression de consanguinité, qui existe principalement dans le cas d'un appariement avec un proche apparenté (Bittles 2001; Jorde 2001; Das 2005; Postma, Martini et al. 2010). Mais ce type d'appariement est limité par d'autres mécanismes psychologiques, tel que l'effet Westermarck qui supprime l'attrance sexuelle entre les individus ayant été élevés ensemble

Encadré 5. Variations intra-individuelles

Nous avons vu que certaines préférences variaient entre les individus. Il existe également des variations au cours de la vie d'un même individu.

De telles variations intra-individuelles sont particulièrement marquées chez les femmes, dont les préférences envers différents éléments de l'attractivité masculine varient au cours du cycle menstruel. Des variations des préférences au cours du cycle ont, entre autres, été reportées pour la masculinité du visage (Penton-Voak, Perrett et al. 1999; Penton-Voak & Perrett 2000; Johnston, Hagel et al. 2001; Little, Jones et al. 2007) et de la voix (Puts 2005; Feinberg, Jones et al. 2006).

Ce phénomène serait lié au compromis entre bénéfices directs et indirects auquel les femmes doivent faire face lors du choix d'un partenaire. En effet, la masculinité est un indice de bonne qualité génétique (Thornhill & Gangestad 1993), mais est négativement corrélée à l'investissement paternel (Perrett, Lee et al. 1998). Les femmes seraient donc plus attirées par les hommes susceptibles de transmettre de *bons gènes* à leurs descendants (bénéfices indirects) au moment où elles sont le plus fertiles, et par des indices liés à l'investissement paternel (bénéfices directs) pendant la phase moins fertile du cycle (Jones, DeBruine et al. 2008).

De plus, les critères d'attractivité physique changent pour une femme selon qu'il s'agisse de choisir un partenaire à court terme ou à long terme. Les caractéristiques liées aux bénéfices indirects sont privilégiées pour un partenaire à court terme, et les indices de bénéfices directs sont préférés pour un partenaire à long terme (Little, Jones et al. 2002; Little, Cohen et al. 2007; Scott, Swami et al. 2008).

Il existe moins de variations intra-individuelles pour les hommes. L'attractivité d'une femme reste toujours liée aux indices de fertilité, même si l'*intensité* (mais non le sens) des préférences masculines peut varier en fonction du contexte (court ou long terme (Li & Kenrick 2006)), ou du taux de testostérone (Welling, Jones et al. 2008).

(Wolf 1970; Vandenberghe 1983; Walter & Buyske 2003; Lieberman, Tooby et al. 2007), ainsi que par des tabous sociaux (Bittles, Mason et al. 1991). Il existe probablement une distance génétique idéale entre les partenaires, ni trop faible ni trop grande, qui pourrait être atteinte grâce à une préférence pour des individus non-apparentés présentant des caractéristiques phénotypiques similaires. Et en effet, des corrélations positives ont été trouvées entre les membres d'un couple pour un grand nombre de traits, comme le milieu culturel, le statut socio-économique, la personnalité, les capacités intellectuelles, et l'apparence physique (Hinsz 1989; Jaffe & Chacon-Puignau 1995; Bereczkei & Csanaky 1996; Keller, Thiessen et al. 1996; Bereczkei, Gyuris et al. 2002; Bereczkei, Gyuris et al. 2004; Little, Burt et al. 2006; Tognetti, Berticat et al. 2014). Enfin, une homogamie au niveau du génome dans son ensemble a récemment été démontrée (Domingue, Fletcher et al. 2014). Cependant, la formation observée des couples ne reflète pas forcément les préférences. Par exemple, si le choix d'un partenaire se fait au sein d'une classe sociale donnée (Solis, Pullum et al. 2007; Dribe & Lundh 2009; Hartung, Vandezande et al. 2011), cela va automatiquement engendrer une homogamie pour les facteurs spécifiques à chaque classe. La compétition pour l'accès aux partenaires va également générer de l'homogamie pour les traits préférés par tous, comme la beauté physique (Courtiol, Picq et al. 2010). Une homogamie au niveau des préférences a pour l'instant été démontrée pour le visage (DeBruine 2004; Saxton, Little et al. 2009; Kocsor, Rezneki et al. 2011) et la taille (Courtiol, Picq et al. 2010). Enfin, l'homogamie semble avoir des effets sur la valeur sélective. Plusieurs études ont montré que lorsque les membres d'un couple se ressemblent au niveau de l'apparence physique, de l'âge, de l'éducation, de la personnalité, ils restent ensemble plus longtemps, sont plus satisfaits de leur mariage et ont plus d'enfants que les couples non homogames pour ces traits (Mascie-Taylor 1988; Bereczkei & Csanaky 1996; Luo & Klohnen 2005). Une étude Islandaise a également trouvé une corrélation positive

entre apparemment et fertilité : les partenaires étant cousins au troisième ou quatrième degré ayant plus d'enfants que les époux génétiquement plus proches ou plus éloignés (Helgason, Snaebjörn et al. 2008).

I.4. Objectifs et plan de la thèse

Nous avons vu que la morphologie de nombreux traits physiques était déterminée par des profils physiologiques et hormonaux qui influencent également la fertilité. Les caractéristiques physiques renseignent donc directement sur la qualité d'une femme en tant que partenaire, et jouent un rôle important dans le choix du partenaire. Bien évidemment, de nombreux autres facteurs (psychologiques, sociaux, culturels...) entrent également en jeu lors du choix d'une partenaire. Cependant, durant cette thèse, seuls les éléments influençant l'attractivité physique des femmes seront examinés. Les questions traitées, soulevées dans la première partie, sont :

1. Comment les hommes détectent-ils les indices de fertilité immédiate ?

Ce point concerne particulièrement le ratio taille/hanche (WHR), un indice de fertilité bien connu mais dont l'importance dans l'attractivité féminine est actuellement remise en question. Une expérimentation basée sur l'analyse des mouvements oculaires (eye-tracking) a été conçue afin de déterminer l'utilisation de cet indice visuel par les hommes lors de jugements d'attractivité.

2. Les hommes détectent-ils et préfèrent-ils les indices de fertilité résiduelle ?

La question était de savoir si les hommes sont sensibles à un autre composant de la qualité

en tant que partenaire, la fertilité résiduelle, déterminée en partie par l'âge à la ménopause. Cette étude a été réalisée en France, sur la base de tests d'attractivité de visages de jeunes femmes.

Dans un deuxième temps, la question de l'universalité des critères d'attractivité féminine sera abordé :

3. Les préférences masculines varient-elles dans l'espace ?

Cette question a été traitée à propos de la fertilité résiduelle. Une étude similaire à celle réalisée en France a été menée en Indonésie, dans une société aux conditions écologiques, sociales et culturelles différentes.

3. Les préférences masculines varient-elles au cours du temps ?

Comme nous l'avons vu dans la première partie, cette question a déjà été abordée par plusieurs études, en particulier pour le WHR. Cette approche a ici été étendue à une large période temporelle, grâce à l'analyse du WHR de femmes représentées dans les Arts depuis la Grèce antique jusqu'à nos jours.

3. Les préférences masculines varient-elles entre individus ?

Dans une société donnée à une époque donnée, les hommes s'accordent-ils tous sur les mêmes critères de beauté ? Cette fois, nous avons étudié des traits physiques non liés à la fertilité. Cette étude, portant sur les traits «neutres» du visage, a été réalisée en France.

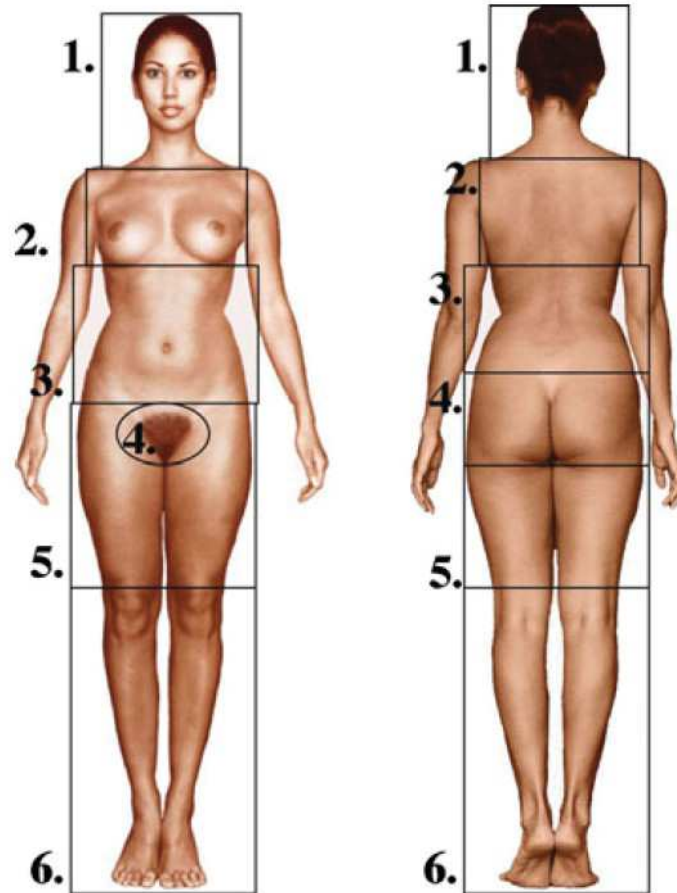


Image 1. Exemple de zones d'intérêt utilisées dans les études utilisant les techniques d'eye-tracking (tiré de Dixson, Grimshaw et al. 2010).

II. Les indices de fertilité

II.1. La fertilité immédiate (Article 1)

Comme nous l'avons vu dans la première partie, parmi les traits influençant l'attractivité du corps féminin, la quantité de graisse corporelle (estimée par le BMI) et sa répartition (estimée par le WHR) jouent un rôle primordial (Singh 1993; Singh & Luis 1995; Furnham, Tan et al. 1997; Henss 2000; Singh 2004; Buunk & Dijkstra 2005; Singh & Randall 2007; Platek & Singh 2010; Singh, Dixson et al. 2010). Cependant, ces études comportementales ne nous disent pas quelles parties du corps sont utilisées par les hommes pour juger l'attractivité d'une femme. La technique de l'eye-tracking (oculométrie en français) représente un nouveau moyen d'investigation pour les études du choix du partenaire, et a récemment été utilisée pour mesurer l'attention visuelle accordée aux différents traits physiques lors du jugement de l'attractivité d'un corps féminin. Ces études ont montré que les hommes dirigent leur attention vers les zones du visage, de la poitrine et du ventre (Suschinsky, Elias et al. 2007; Hewig, Trippe et al. 2008; Dixson, Grimshaw et al. 2009; Dixson, Grimshaw et al. 2010). Ces études utilisent des zones d'intérêt (region of interest : ROI), qui segmentent l'espace visuel (ici une image de corps de femme), afin de simplifier les analyses. Ces zones d'intérêt sont sensées représenter des catégories visuelles pertinentes (une zone comprend par exemple la tête, la poitrine, ou les jambes, voir image 1).

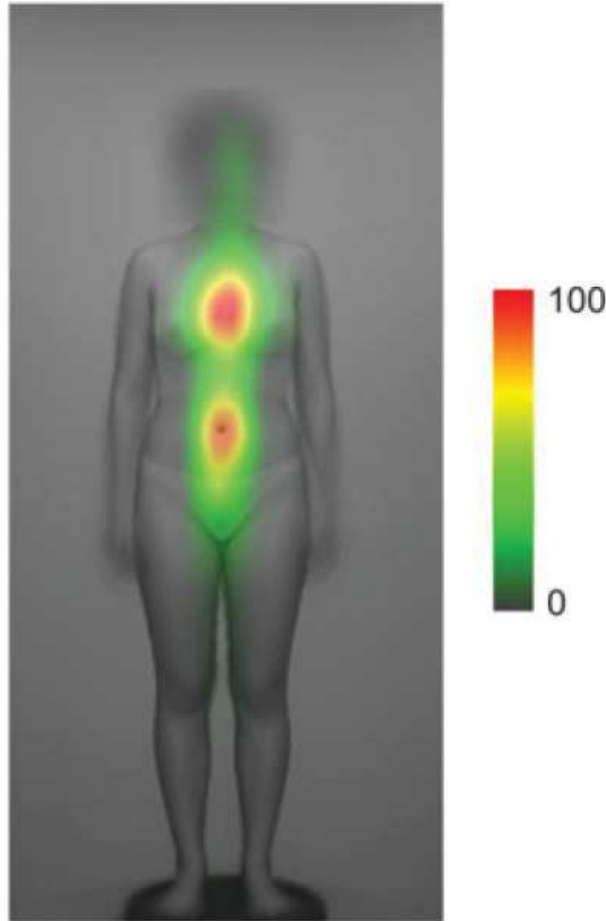


Image 2. Résultats de l'étude de Cornelissen, Hancock et al. (2009). Densité de fixations lors d'un jugement d'attractivité (la couleur rouge indique une forte intensité de fixation).

Cependant, la segmentation de l'espace visuel est faite de manière subjective par l'expérimentateur, ce qui est évidemment problématique d'un point de vue scientifique (Caldara & Miellat). De plus, les zones d'intérêt utilisées dans ces études sont souvent grandes (la région du torse peut aller de la poitrine jusqu'à la taille par exemple), ce qui diminue fortement la résolution spatiale, et peut conduire à la non détection de certains mouvements du regard.

Pour éviter ces limitations, il existe une nouvelle méthode ne nécessitant aucune segmentation de l'image, inspirée des techniques utilisées en imagerie par résonance magnétique fonctionnelle (Caldara & Miellat). Cette technique permet d'identifier de façon précise les régions du corps observées lors d'un jugement d'attractivité. La seule étude utilisant cette technique a donné des résultats inattendus : le regard des participants était concentré au centre du torse (au niveau de l'estomac et du sternum), une région non connue pour influencer l'attractivité féminine (Cornelissen, Hancock et al. 2009, voir image 2).

Mais les fixations du regard mesurées par l'eye-tracking ne représentent pas avec exactitude l'information extraite lors de l'observation. En effet, il est possible que l'information captée par la vision périphérique, même si elle est de basse résolution, suffise pour évaluer la forme générale du corps. Ainsi, en restreignant l'information située à l'extérieur de la zone centrale de fixation, il a été montré que l'information réellement utilisée pour la reconnaissance d'un visage était la même entre différents groupes humains, alors même que la stratégie utilisée pour extraire cette information était très différente (Caldara, Zhou et al. 2010).

Dans cette étude, nous avons adapté cette technique de restriction de la vision périphérique à un contexte de choix du partenaire. Trente-cinq participants de sexe

masculin ont estimé l'attractivité de corps féminins générés par ordinateur, sous différentes conditions d'observation : une condition en *vision naturelle* et 2 conditions de type *spotlight*. Dans la condition en *vision naturelle* (NV), l'image était visible en entier. Pour les conditions *spotlights*, l'image était visible à travers une ouverture circulaire d'un diamètre de 2° ou 4° d'angle visuel, se déplaçant sur l'écran avec le regard de l'observateur. Les corps féminins, dont le WHR et la tête variaient, étaient présentée une fois de face et une fois de dos. L'ordre des conditions et des images au sein de chaque condition étaient aléatoires.

Les résultats de cette étude démontrent que les hommes utilisent leur vision périphérique pour estimer l'attractivité d'un corps féminin. Les conditions d'observation avaient un effet significatif sur le schéma d'observation : lorsque l'accès à l'image était restreint à une petite ouverture, les hommes regardaient plus longtemps les contours extérieurs du torse, au niveau des seins (pour les vues de face), et des hanches (pour les vues de face et de dos), alors qu'ils privilégiaient le centre de ces zones lorsque le corps entier était visible. Ce résultat suggère que l'information nécessaire à l'estimation de l'attractivité féminine peut être acquise sans fixer les contours du torse directement (lorsque la vision périphérique est disponible), mais que l'information présente au centre du corps n'est pas suffisante en elle-même. L'information récoltée grâce à la vision périphérique pourrait être la courbure de la silhouette, liée au WHR. Les résultats de cette étude mettent aussi en évidence le rôle crucial, dans l'estimation de l'attractivité féminine, de la largeur des hanches, qui pourrait représenter un indice du BMI.

ARTICLE 1

Mapping females' bodily features of attractiveness

Jeanne Bovet, Junpeng Lao, Océane Bartholomé, Roberto Caldara, Michel Raymond

Soumis

Mapping females' bodily features of attractiveness

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Abstract

“Beauty is bought by judgment of the eye” (Shakespeare, *Loves Labours Lost*), but the bodily features governing this critical biological choice are still debated. Eye movement studies have demonstrated that male sample coarse body regions expanding from the face, the breasts and the midriff, while making female attractiveness judgements with natural vision. However, the visual system ubiquitously extracts diagnostic extra-foveal information in natural conditions, leaving this question unresolved. We thus used a parametric gaze-contingent design while male rated attractiveness of female front- and back-view bodies. Male used extra-foveal information when available. Critically, when bodily features were only visible through restricted apertures, fixations strongly shifted to the hips, to potentially extract hip-width and curvature, then the breast and face. Our hierarchical mapping suggests that the visual system primary uses hip information to compute the waist-to-hip ratio and the body mass index, the crucial factors in determining sexual attractiveness and mate selection.

Keywords: Attractiveness; Waist-to-hip ratio; Body-mass index; Eye tracking; Peripheral vision.

Introduction

Behavioral studies have suggested that body fat (estimated by the body-mass index: BMI) and its distribution (estimated by the waist-to-hip ratio: WHR) play a critical role in the evaluation of female physical attractiveness by men [1-9]. However, none of these studies could directly map out the bodily visual information used by the observers to *actively* achieve this crucial biological categorization for mating, as well as their respective importance in determining this choice. More recently, eye-tracking studies have attempted to address this question by analyzing the fixation patterns deployed to morphological traits when observers are performing attractiveness judgments [10-14]. These studies have shown that when men were evaluating the attractiveness of female bodies, much of their attention was directed to the face, breasts and midriff. Typically, these eye movement studies relied on the use of a Region or Area of Interest (ROI or AOI) approach for statistical analyzes, which reduce the high-dimensional visual input space (thousands or millions of pixels of the presented image) into a low-dimensional space. Although ROIs are implicitly assumed to optimally represent the visual categories present in the visual input space (e.g., the face, breasts, midriff and leg regions), they suffer from an arbitrary and *subjective* segmentation of the visual inputs into ROIs, which are constrained by the a priori biases of the experimental framework and experimenters [15]. In the present context, ROIs used in attractiveness studies are thus often over-represented, and their boundaries are difficult to determine (e.g., the midriff area extends from the below the breasts to the widest part of the hip [13, 14]). This shortcoming leads to a considerable loss of spatial resolution, with arbitrary categorization of eye movements falling on the ROIs' borders and the loss of subtle patterns of eye movements between ROIs [10, 11, 13, 14]. Another critical drawback of previous eye movement studies is their reliance on the use of natural vision paradigms for determining fine-grained visual information use because the visual system can extract diagnostic information without focal fixations. For instance, Kuhn and Tatler [16] have shown that people can detect the misdirection in a magic performance without fixating on the precise location where the trick is taking place. Similar findings demonstrate that information extracted from a foveal fixation during natural viewing does not straightforwardly translate to

information use. As a consequence, the question of which bodily features are used by men during the evaluation of female attractiveness remains unresolved.

To address this question, we recorded the eye movements of male observers during attractiveness judgments by combining a data-driven analysis (i.e., *iMap 4* [15]) and a gaze-contingent design [17]. *iMap 4* implements a Linear Mixed-Model (LMM – see methods) with a robust statistical approach to correct for the multiple comparison problem driven by repetitive testing in the pixel space. *iMap 4* was thus used to *objectively* define the regions of the body fixated by men's judgments of female attractiveness; no a priori image segmentation is required with this technique. To finely estimate information use, we used a conventional natural viewing paradigm and also gaze-contingent paradigms in which the stimulus display is continuously updated as a function of the observers' current gaze position. We parametrically restricted the bodily information available to the observers by using 'Spotlights' with 2° (foveal vision only) or 4° apertures dynamically centered on observers' fixations to isolate information use. Crucially, the 2° Spotlight apertures covered a single bodily feature (i.e., face, breast or hip), while the 4° condition was closer to natural viewing conditions: information from the outline of the body could be available to the observers when they fixed at the center of the torso. Participants rated the attractiveness of front- and back-view computer-morphed women's bodies under these three viewing conditions.

Concordant with previous studies, attractiveness ratings were influenced by face [18, 19], WHR [1-9] and hip size [20, 21]. As expected, observers directed their gaze towards the women's stomachs and to the central part of the chest (sternum) during natural vision, corroborating previous findings [12]. However, these physical features (sternum and stomach) are not known, in the literature, to influence female attractiveness. When the front-view body images were visible only through a restricted aperture (*Spotlights*), the observers' fixations were still directed to the women's face/head, but also progressively shifted to the breasts and the hips. Importantly, the hip area was the only bodily feature invariantly used to perform judgments of attractiveness with front- and back-view bodies, showing the largest fixation increase among the critical features involved in physical attractiveness.

This observation posits the hips as being the critical diagnostic region for evaluating female attractiveness.

Methods

Stimuli. Virtual female bodies were created with the MakeHuman software, which allows for the flexible morphing of a 3D human body that varies in several dimensions (see Figure 1). Three waist and 2 hip circumferences were used, resulting in 6 different body shapes representing a relatively large range of WHR (0.67-0.87) within a reduced range of BMI. To avoid an eventual habituation effect, 3 distinct faces (with different haircuts and facial features) were combined with each body shape, resulting in a total of 18 unique virtual female bodies. All other features were kept constant. The WHR of each 3D stimulus was calculated with the software measures. The volume (in cm³) of each stimulus was measured using the plugin Viewer 3D of ImageJ. Screenshots of female bodies were exported with three different views: front and back, corresponding to a total of 36 images (6 WHR * 3 faces * 2 positions).

Participants. Thirty-five male observers participated in the current study. For each observer, the following information was collected: age, monthly income, and education level. The participants' ages ranged from 20 to 39 (average 25 years old). The volunteer raters were unaware of the purpose of the study when assessing the artwork.

Ethics Statement. Public advertisements were dispatched in local stores and social networks to recruit volunteers. These advertisements contained the principle of the test (an eye-tracking study on female attractiveness) and our contact information. The protocol used to collect and analyze data was approved (#1226659) by the French National Committee of Information and Liberty (CNIL). For each participant, the general purpose of the study was explained, and a written voluntary agreement was requested for a statistical use of the data. Each participant received a compensation of 20€. The data were analyzed anonymously.

Procedure. The experiment was carried out in an isolated room under uniform lighting conditions. The observers were seated in a chair, facing the screen at a distance of 83 cm. The viewing distance was

maintained with a forehead and chin rest. The experiment was programmed in SR Research Experiment Builder (version 1.10.1025) and ran on a 3-GHz core i7 computer. The stimuli (924 pixel height) were presented on a 19-inch screen at a 1280x1024 resolution with a refresh rate of 60 Hz. The experiment was divided into 3 blocks corresponding to 3 different viewing conditions: a *natural viewing* condition and 2 *spotlight* conditions. For the *natural viewing* condition, the whole picture was displayed (see Figure 1). For the *spotlight* conditions, the picture was visible through a gaze-contingent circular aperture with a diameter of either 2° or 4° (see Figure 2). Each body was presented once from a front-view and once from a back-view within each block (see Figure 1). The aperture edges were blurred, and the visual field outside the aperture was black. The 3 blocks were conveyed in random order for each observer. Within each block, the 36 body images were presented in a random sequence either on the left or the right of the screen to avoid any anticipatory eye movement. The image remained on the screen until the observers pressed the space bar. The participants rated the body attractiveness using a keyboard with an 11-point scale (0 being the least and 10 the most attractive) at the end of each trial. A white dot was presented in the middle of the screen in between each presentation for drift correction.

Eye Tracking. Using the EyeLink® 1000 Desktop Mount system (SR Research Ltd., Ontario, Canada), eye position and eye movements were determined by measuring the corneal reflection and dark pupil with a video-based infrared camera and an infrared reflective mirror. The eye tracker had a spatial resolution of 0.01° of the visual angle, and the signal was sampled and stored at a rate of 1000 Hz. Although the viewing was binocular, the recording was monocular (a standard procedure in eye-tracking studies). Calibration and validation of the measurements were performed before each experimental session.

Behavioral analyses. For each condition, we applied a logistic mixed model to analyze observers' subjective ratings. The WHR of female bodies was considered to be the main explanatory variable. There were 3 different faces and 2 different hip sizes for each waist size. We thus integrated the face types and hip sizes as additional explanatory variables in the model. The position (front or back) was entered as a confounding effect. Variables concerning the observers' characteristics (age, monthly

income, and education level) were also included in the model as potential confounding effects. Each individual female image and the observers were considered as random-effect variables. Overall, our logit mixed model could be expressed as the following:

$$\text{Logit}(\text{Rating}) \sim \text{WHR} + \text{Hip size} + \text{Face} + \text{Body orientation} + \text{Observer age} \\ + \text{Observer income} + \text{Observer education} + (1 | \text{Image}) + (1 | \text{subject})$$

The logit mixed model was fitted with LMER using R 3.1.1 (R Core Development Team).

Eye movement analyses. Eye movement data were analyzed using the new version of *iMAP*¹ [15], which implements a robust data-driven approach based on a Linear Mixed Model (LMM) and a bootstrap clustering method for hypothesis testing. Fixations and saccades were extracted from the raw data by using the default settings in the Eyelink software. Fixation durations were then projected back into the two-dimensional space according to their x and y coordinates at the single trial level. We smoothed the fixation duration map by convoluting it with a two-dimensional Gaussian Kernel function.

$\text{Kernel} \sim N(0, \sigma^2 I)$, where I is a two by two identity matrix and $\sigma/2 = 1^\circ$ visual angle.

We then estimated the fixation bias of each condition independently for all the observers by taking the expected values across trials within the same condition. The resulting 3D matrix (Conditions*xSize*ySize) was then modeled in a LMM as the response variable. Subjective ratings were also computed by taking the average for each condition. To quantify the spatial bias in the fixation pattern for each experimental manipulation, the intensity of each pixel in the smoothed duration map was modeled with the following LMM specification:

$$Y_{(x,y)} \sim \text{Rating} + \text{Viewing condition} + \text{Body orientation} + \text{Viewing condition} * \quad (1) \\ \text{Body orientation} + (\text{fixation duration} | \text{subject}) \quad 1 \leq x \leq x\text{Size}, 1 \leq y \leq y\text{Size}$$

Thus, the fixation duration was considered as a function of *subjective rating*, *viewing condition* (3 levels), *body orientation* (2 levels), and the *interaction between the categorical predictors*. In addition, the mean fixation duration for each condition and the intercept were treated as random effects to

¹ This version (iMap 4) has not yet been released to the public domain.

control for the variation across individuals. An alternative model is also fitted to the fixation maps to better estimate the categorical predictors as follows:

$$Y_{(x,y)} \sim \text{Viewing condition} + \text{Body orientation} + \text{Viewing condition} * \text{Body orientation} + (\text{fixation duration} \mid \text{subject}) \quad 1 \leq x \leq xSize, 1 \leq y \leq ySize \quad (2)$$

The LMM was fit by maximal likelihood (ML) using the *fitlme* function from the Statistics Toolbox™, Matlab 2013b. Furthermore, the sum of all categorical coefficients in the design matrix were set to zero to allow type III hypothesis testing in analyses of variance (ANOVA). Parametric statistics on the fixed effect and contrasts are performed by the *coefTest* for LinearMixedModel class in the Matlab software. To control for false positives from pixel-wise hypothesis testing, a multiple comparisons correction was applied by using a bootstrap clustering method [22, 23]. Original parametric statistical values were thresholded at a given p value ($0.05 / \text{the number of pixels}$). We then calculated the cluster mass by summing the statistic values within each cluster and later compared them with a bootstrap distribution under the null hypothesis. To construct the bootstrap null distribution, the condition mean is removed from each categorical condition and randomized without replacement to disrupt any possible covariation between fixation intensity and attractiveness ratings. This procedure makes sure that $H_0: \mu=0$ is true for all potential coefficients while preserving the global variance for the experiment conditions. A subject-wise bootstrap with replacement was then repeated 1000 times to create a set of bootstrap null response matrices. We then performed the same modeling and subsequently the same contrast tests for the selected coefficients across all pixels. The resulting statistical map for each bootstrap was thresholded with the same parameters of the original map. The maximum cluster mass in each bootstrap was put into a vector and then sorted to form a bootstrap distribution for each contrast. Given that bootstrapped response matrices are derived under the null hypothesis, the cluster-wise p -value was calculated as:

$$p = 1 - \frac{\sum(\text{cluster mass} \geq \text{bootstrap cluster mass})}{\text{num of bootstrap}} \quad (3)$$

which results in the cluster-corrected p values.

Results

Behavioral analyses. The result from the logit mixed model showed a significant negative relationship between WHR and attractiveness ratings in both *natural viewing* and 4° *spotlight* conditions ($\beta_{\text{natural viewing}} = -5.78$ [-7.43; -4.13] and $\beta_{4^\circ \text{ spotlight}} = -3.78$ [-5.28; -2.27], $p < 0.0001$, respectively, see supplementary table S1; square brackets report the 95% confidence interval). However, the relationship between the two was not significant in the 2° *spotlight* condition ($\beta_{2^\circ \text{ spotlight}} = -0.83$ [-2.33; 0.65], $p = 0.30$). Observers rated female bodies with a low WHR more favorably when they had access to sufficient peripheral vision. The hip size had a significant negative effect on the attractiveness ratings for all the conditions ($\beta = -0.13$ [-0.14; -0.11], -0.05 [-0.06; -0.03] and -0.02 [-0.03; -0.007], respectively, for the *natural viewing*, 4° and 2° *spotlight* conditions, $p < 0.01$). Female bodies with overly large hip sizes received a lower attractiveness rating regardless of *viewing conditions*. The face also significantly influenced the subjective ratings for all the conditions ($p < 0.0001$). The position effect of the female body (front or back) was significant for the *natural viewing* and 2° *spotlight* conditions ($\beta = 0.16$ [0.01; 0.31] and -0.14 [-0.28; -0.01], respectively, $p = 0.045$ for both), but not for the 4° *spotlight* condition ($\beta = 0.07$ [-0.06; 0.21], $p = 0.27$). None of the observers' characteristics (age, monthly income, or education level) showed modulation on their ratings ($p > 0.05$).

Eye movements. After the initial model fitting, pixel-wise ANOVA on the Linear Mixed-Model with a full design (LMM – equation 1 in the methods section) revealed significant main effects for both viewing condition and body orientation (see supplementary Figure S1) after using a bootstrap clustering procedure to correct for multiple comparisons. The interaction did not reach significance. Importantly, the main effect of the viewing condition is shown around the hips (Peak: $F(2,195) = 45.72$, minimal: $F(2,195) = 18.99$, $p < 0.05$ cluster corrected), while a significant effect of the body orientation is clustered around the face region (Peak: $F(1,195) = 119.01$, minimal: $F(1,195) = 33.46$, $p < 0.05$ cluster corrected). The main effect of subjective attractiveness ratings was not significant, suggesting that there is no obvious relationship between the time spent on the body areas fixated and the judgments of attractiveness.

To further clarify these findings, we estimated the coefficients for each categorical predictor on the LMM with a categorical model (see equation 2 in methods section). As shown in Figure 3, observers fixated on the face region when the body was present in the full front position, regardless of the visual field size (local maximum on the face area in front view condition: $\beta_{\text{natural viewing}} = 273.8$ [107.7, 445.9], $\beta_{4^\circ \text{ spotlight}} = 461.5$ [284.5, 638.5], $\beta_{2^\circ \text{ spotlight}} = 639.7$ [465.1, 814.4]). As a comparison, the hip areas were fixated longer in the 2° spotlight condition regardless of the body orientation (local maximum of 2° spotlight condition: $\beta_{\text{front view}} = 228.2$ [169.7, 286.8], $\beta_{\text{back view}} = 273.3$ [214.7, 338.8]). Finally, to obtain a fine-grained picture of information use, we performed a pixel-wise linear contrast between the 2° spotlight condition and the natural viewing conditions (see Figure 4 left panel, contrast test F-value at peak: $F(1,195) = 79.10$, minimal: $F(1,195) = 33.42$, $p < 0.05$ cluster corrected). This analysis revealed that the upper part of the face, the breast and the hip areas are the key bodily features sampled for performing attractiveness judgments. To further quantify the relative importance of information among these areas, we computed post-hoc analysis within each significant area (i.e., face, breast and hip area) from the linear contrast. We computed the normalized contrast of any two given front-view conditions by dividing the contrast of the peak values by their sum within each body area. As shown in the right panel of Figure 4, the weight contrast from the hip area changed the most rapidly as compared to other body regions ($F(2,285) = 19.249$, $p < 0.05$).

Discussion

Here, we show that men use their peripheral vision to assess the attractiveness of female bodies. The gaze-contingent aperture size significantly affected the way men look at female bodies: when observers could access visual information only through a narrow aperture, they gazed more at the exterior edges of the torso – the hips – (front and back view) and the breast (front view), while during natural viewing they favored the center of these regions as they could process the entire silhouette from this location. Altogether, these results indicate that the information necessary to estimate female attractiveness can be gathered without directly staring at the contours of the hips when peripheral vision is available, but clearly the center of the torso itself is *not* containing diagnostic information.

Interestingly, our data also showed the largest increase in fixations towards the hips during the 2° foveal vision condition (for both front-and back-views), followed by the face and the breast with front-views, giving this region a pivotal role in the evaluation of female attractiveness. The information collected in this area could relate to the extraction of the curvature of the hip shape and an estimation of hip width, as highlighted by the fixation patterns with constrained vision. In fact, WHR had an effect on the attractiveness ratings only when the peripheral vision was sufficient (in the *natural viewing* and 4° *spotlight* conditions), which is concordant with the fact that the whole silhouette is necessary to estimate the WHR [12].

Why use peripheral vision when relevant information could be extracted directly? Although information is crucial to adaptive decision-making, only a fraction is actually relevant to the task; even so, individuals tend to encounter information at rates considerably higher than their capacity for full use [10]. Attentional resources are necessary for discriminating useful from irrelevant information, but they are limited and so should be allocated selectively. The use of peripheral vision could result in an optimal decision-making system: individuals able to extract only relevant information from the body shape, without amassing superfluous details, will make decisions rapidly and expend less energy in the process. Nevertheless, our study is restricted to a Caucasian population. It is possible that, as for the recognition of faces [17, 24], the use of peripheral vision in the assessment of female attractiveness varies between populations. Further investigation is needed to determine the universality--or variability--of men's eye movement patterns in female attractiveness judgments.

In line with previous findings, a large number of fixations were directed towards the face in the front-view condition [13], and to a lesser extent to the head during the back-view condition [14]. Viewing facial features in the front-view had a significant influence on attractiveness ratings [18, 19]. However, the greatest numbers of fixations were directed towards the hip regions with restricted vision, and their width was the most important determinant of attractiveness, independently from the WHR. This shift toward the external part of the torso was weaker for the waist, confirming that information provided by the hip is more important than the information included at the waist level. Additionally, hip size had a significant effect on attractiveness ratings in all viewing conditions. The

importance of hip size for attractiveness, independently of WHR, has been previously reported [20, 21]. What is the information conveyed by hip size? Large hips could give the impression of a heavier body [4]. Indeed, body width, and especially the lower torso width, is a reliable guide to BMI [25]. As the hip contours are required to estimate their width, the relevant information of this region (normally provided by the peripheral vision) could be the BMI or a related measure. The BMI is also correlated with health and fertility [26-30]. The BMI may be a factor equivalent to--or even more important than--the WHR in determining the physical attractiveness of a woman [20, 21, 25, 31]. The extraction of women's WHR information could have an evolutionary basis because WHR is a reliable indicator of a women's age, health and fertility: Compared to women with high WHR, women with a low WHR have fewer irregular menstrual cycles [32], optimal sex hormone profiles [33], ovulate more frequently [34], and have lower endocervical pH, which favors sperm penetration [35]. Low WHR is also an independent predictor of pregnancy in women attending an artificial insemination clinic [36] and in women attempting in-vitro embryo fertilization transfer [37].

In summary, our data show that men use their peripheral vision in judgments of female attractiveness under natural viewing conditions. This could allow for the estimation of the WHR, even without directly staring at the curve of the torso. Additionally, analyses of both attractiveness ratings and eye movements isolated a hierarchy of cue use, positing the hip width as an important feature of female attractiveness, independent from the WHR. The hip width could also be a key feature in estimating the BMI, another trait linked with a woman's health and fertility. Overall, this bodily feature seems to play a critical role in the evaluation of female attractiveness by men and offers novel insights into the critical visual information beneath the contemporary obsession with being thin.

Author Contributions

J. Bovet, R. Caldara and M. Raymond developed the study concept. All authors contributed to the study design. Data collection was performed by O. Bartholomé and J. Bovet. J. Bovet and M. Raymond performed the behavioral data analysis. R. Caldara and J. Lao performed the eye movement

analysis. J. Bovet, J. Lao, R. Caldara and M. Raymond wrote the manuscript. All authors approved the final version of the manuscript for submission.

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Figures



Figure 1. Front- and back-views of a stimulus under the *natural viewing* condition.

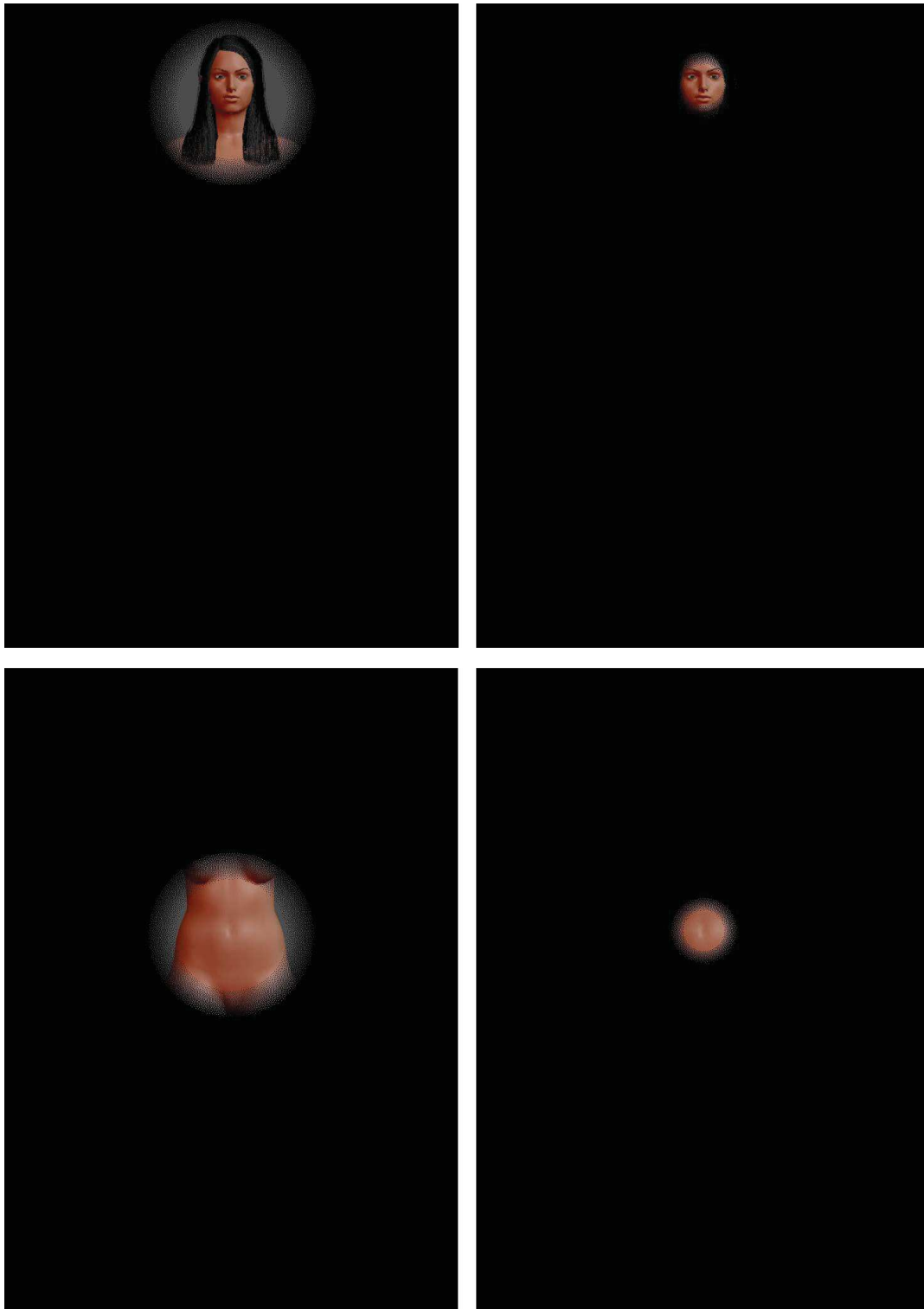


Figure 2. Front views of one stimulus on the two *Spotlight* conditions, with gaze-contingent apertures of 4° (first column) and 2° (second column) centered on the face (first row) and on the navel (second row). The aperture of 2° covered the entire face, but the edges of the torso were not visible when fixating the navel. The aperture 4° allowed one to simultaneously see the edges of both sides of the torso when fixating the navel.

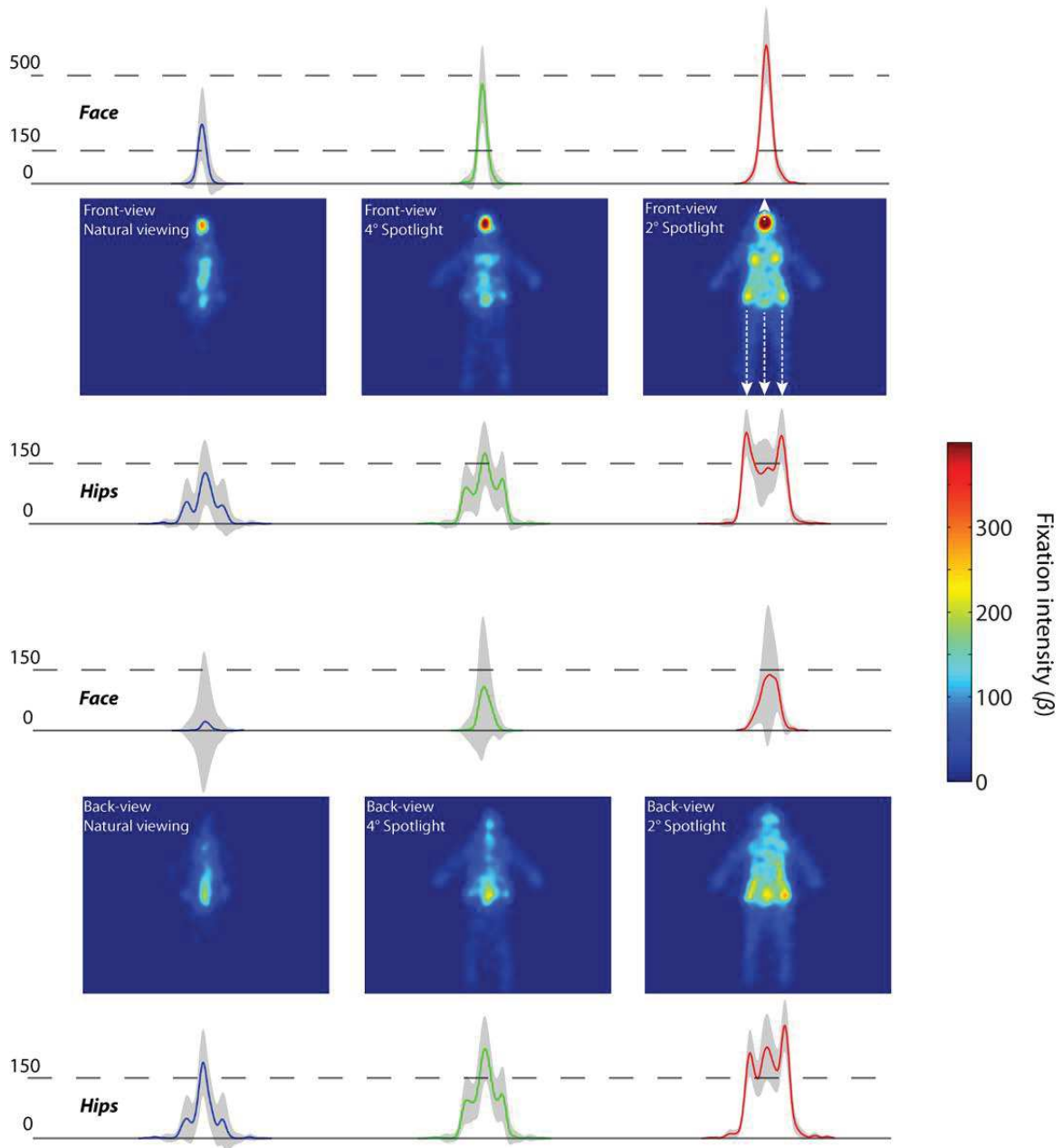


Figure 3. Estimated 2D coefficient (β) maps and their local maximum on the face and hip areas for each categorical predictor of the LMM (Eq. 2). Line plots of the beta values were extracted from the x axis containing the local maxima for the face and hip regions. The 95% confidence intervals are reported in the grey areas.

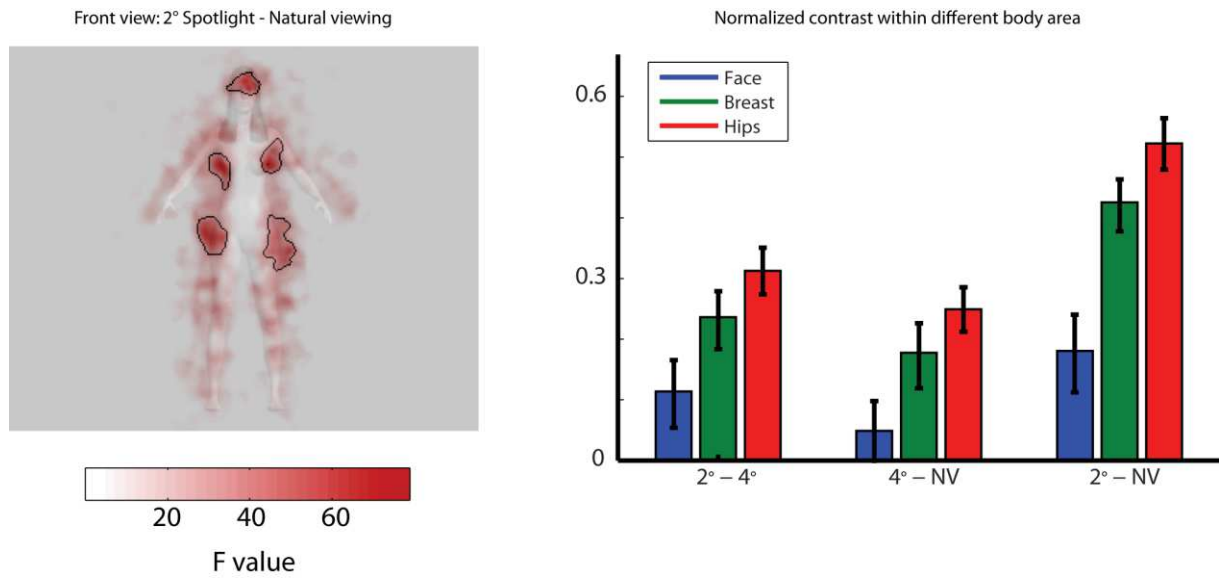


Figure 4. Left panel: difference fixation maps performed on the LMM (Eq. 2) between the front view 2° spotlight and natural viewing conditions. Significant clusters are outlined with black lines. Right panel: normalized contrast among the three viewing conditions within different region masks from Left panel. Error bars report standard errors.

Supplementary

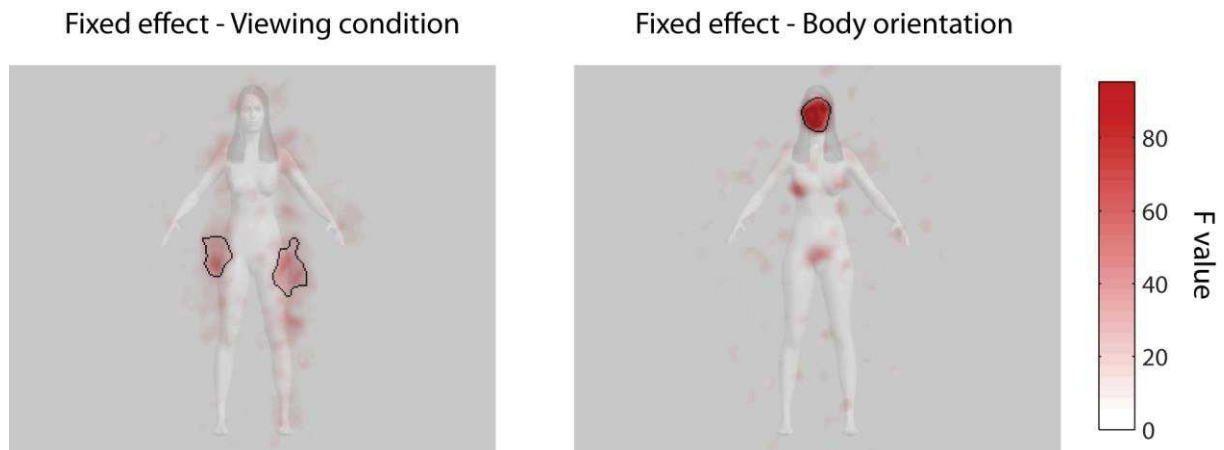


Figure S1. ANOVA result on LMM (Eq. 1). Left panel: F-value map of the viewing condition factor. Right panel: F-value map of the body orientation factor. Significant clusters are outlined with black lines (cluster corrected $p < .05$).

Table S1.

Results of the logit mixed model for the behavioral analysis of the observers' subjective ratings. The intercept corresponds to a front view picture of a female body with an average WHR and hip size, and with the face n°1.

Viewing condition	Variable	Estimate	Confidence interval 95 %	p-value
Natural viewing	Intercept	21.61	[18.10; 25.14]	< 0.0001
	WHR	-5.78	[-7.43; -4.13]	< 0.0001
	Hip size	-0.13	[-0.14; -0.11]	< 0.0001
	Face n°2	-1.41	[-1.59; -1.23]	< 0.0001
	Face n°3	-1.36	[-1.54; -1.18]	< 0.0001
	Position (back)	0.16	[0.01; 0.31]	0.045
	Observer's age	0.05	[-0.03; 0.14]	0.26
	Observer's income	0.09	[-0.08; 0.28]	0.3
	Observer's education	-0.09	[-0.39; 0.20]	0.53
4° spotlight	Intercept	12.27	[9.09; 15.45]	< 0.0001
	WHR	-3.77	[-5.28; -2.27]	< 0.0001
	Hip size	-0.05	[-0.06; -0.03]	< 0.0001
	Face n°2	-1.25	[-1.41; -1.08]	< 0.0001
	Face n°3	-1.34	[-1.50; -1.17]	< 0.0001
	Position (back)	0.07	[-0.06; 0.21]	0.27
	Observer's age	0.06	[-0.009; 0.14]	0.096
	Observer's income	0.003	[-0.15; 0.15]	0.96
	Observer's education	0.07	[-0.186; 0.32]	0.6
2° spotlight	Intercept	9.29	[6.02; 12.57]	< 0.0001
	WHR	-0.83	[-2.33; 0.65]	0.3
	Hip size	-0.02	[-0.03; -0.007]	0.006
	Face n°2	-1.1	[-1.27; -0.94]	< 0.0001
	Face n°3	-1.32	[-1.48; -1.16]	< 0.0001
	Position (back)	-0.14	[-0.28; -0.01]	0.045
	Observer's age	-0.006	[-0.09; 0.08]	0.88
	Observer's income	0.07	[-0.10; 0.25]	0.43
	Observer's education	0.01	[-0.27; 0.30]	0.9

II.2. La fertilité résiduelle (Article 2)

Nous avons vu que la fertilité immédiate, signalée chez la femme par de nombreux indices, était étroitement liée à l'attractivité féminine. Pour le succès reproducteur d'un homme, la fertilité immédiate d'une partenaire est en effet cruciale, surtout dans le cadre d'une relation à court terme. Cependant, pour les relations à long terme (comme le mariage par exemple), la valeur reproductive résiduelle – c'est à dire la fertilité future attendue – devient également pertinente. Cela est renforcé par l'existence, dans l'espèce humaine, d'une sénescence reproductive (la ménopause), correspondant à la fin de la capacité à se reproduire. Chez les femmes, puisque les sénescences reproductives et somatiques sont dissociées, la valeur reproductive résiduelle est indépendante de la longévité. Avec une fenêtre temporelle de reproduction ainsi restreinte, la jeunesse est un critère primordial dans le choix d'une partenaire, puisqu'elle signale une forte valeur reproductive résiduelle. De plus, pour un âge donné, la fenêtre temporelle de reproduction varie en fonction de l'âge à la ménopause, qui est variable dans, et entre, les populations (Thomas, Renaud et al. 2001; Dratva, Real et al. 2009; Morris, Jones et al. 2011; Stepaniak, Szafraniec et al. 2013). Si le futur âge à la ménopause est détectable chez les jeunes filles, il devrait intervenir lors du choix d'une partenaire, et donc influencer l'attractivité féminine.

Le but de cette étude était de voir si la valeur reproductive résiduelle était liée à l'attractivité faciale des jeunes filles. Nous avons présenté, par paires, des photos de 68 jeunes filles entre 25 et 35 ans à 119 juges masculins. Les juges devaient choisir la photo de la jeune femme qu'ils trouvaient la plus attirante. Comme l'âge à la ménopause est héritable (Snieder, MacGregor et al. 1998 ; van Asselt, Kok et al. 2004 ; Murabito, Yang et al. 2005 ; Morris, Jones et al. 2011), l'âge à la ménopause de la mère était utilisé comme

proxy de l'âge à la ménopause attendu des jeunes filles. Nous avons pris comme variables de contrôle des composants déjà connus de l'attractivité du visage (féminité et symétrie), ainsi que des traits liés au taux d'œstrogènes et à la fertilité immédiate (WHR, BMI, fréquence fondamentale de la voix (F0)). Nous avons évidemment pris en compte l'âge des jeunes filles, mais également le vieillissement du visage, estimé par la différence entre l'âge perçu (par un échantillon de participants devant estimer l'âge des jeunes filles à partir de chaque photo) et l'âge réel.

Les résultats de cette étude montrent que l'âge à la ménopause attendu a un effet positif significatif sur la probabilité d'être choisie comme la jeune fille la plus attirante lors de la présentation des pairs de photos : les hommes ont eu tendance à préférer les femmes dont le futur âge à la ménopause (estimé par celui de leur mère) était le plus élevé. Comme attendu, plusieurs variables liées à la fertilité immédiate avaient également un effet sur l'attractivité : Les juges préféraient les femmes plus jeunes, plus symétriques, et ayant une F0 plus élevée. Le vieillissement du visage était aussi négativement corrélé à l'attractivité. Par ailleurs, il n'y avait aucune corrélation entre l'âge à la ménopause attendu et les différentes variables de fertilité immédiate ou d'attractivité (féminité, symétrie, WHR, BMI, F0, vieillissement du visage).

Avec cette étude, nous avons donc montré que l'âge à la ménopause attendu était significativement relié à l'attractivité des jeunes femmes, et qu'il s'agissait d'une information faciale indépendante et non déductible des composants déjà connus de l'attractivité. Si les préférences reflètent réellement les choix de partenaires effectifs, la préférence des hommes pour des femmes signalant un âge élevé à la ménopause (et donc une fenêtre reproductive plus longue), suggère qu'il existe aujourd'hui une sélection envers un recul de l'âge à la ménopause (Il est intéressant de noter qu'effectivement, un certain

recul de l'âge à la ménopause a récemment été observé (vanNoord, Dubas et al. 1997 ; Rodstrom, Bengtsson et al. 2003 ; Dratva, Real et al. 2009)). Reste la question de l'origine et du maintien de la ménopause dans l'espèce humaine, qu'une telle sélection rendrait plus difficiles. Il reste également à identifier quels sont les traits, présents dans le visage des jeunes filles, qui sont reliés à l'âge à la ménopause.

ARTICLE 2

Women's attractiveness is linked to expected age at menopause

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Soumis

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WOMEN’S ATTRACTIVENESS IS LINKED TO EXPECTED AGE AT MENOPAUSE

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22 **Abstract**

23 Why some women have more attractive face than others has been the focus of many studies.
24 For short-term mating, males are expected to prefer females at the age of peak fertility. In fact,
25 facial fertility cues have been linked to female attractiveness. For long-term partnerships, a
26 high residual reproductive value - the expected future reproductive output - becomes more
27 pertinent; thus, young age and late menopause are expected to be preferred. However, the
28 extent to which facial features provide cues to the likely age at menopause is unknown. Here,
29 we show that expected age at menopause is linked to facial attractiveness of young women.
30 As menopause is heritable, we used the mother's age at menopause as a proxy for the
31 daughter's expected age of menopause. We found that men judged facial photographs of
32 women with a later expected age at menopause as more attractive than those of women with
33 an earlier expected age at menopause. This result holds when age and other components of
34 facial and non-facial attractiveness were controlled. Additionally, we found that the expected
35 age at menopause was not correlated with any of the other variables considered (including
36 facial ageing, fertility and developmental cues). Our results show the existence of a new
37 correlate of women's facial attractiveness, expected age at menopause, which is independent
38 from previously documented components of attractiveness.

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43 Key words: mate choice, female attractiveness, face, menopause, residual reproductive value

44 **1. Introduction**

45 Why some women are more attractive than others has been the focus of many studies, and it
46 has been repeatedly shown that features linked to fertility explain a large part of the variance
47 in attractiveness [1]. Cues of fertility can be found in body shape, voice pitch, or facial
48 features; in fact, all traits substantially influenced by sex hormones during growth and puberty
49 have the potential to influence physical attractiveness [2-8]. In addition, traits reflecting
50 favourable developmental stability, such as bilateral symmetry, are also associated with
51 increased female attractiveness [9-11].

52 Males should prefer females of the age at which age-specific fertility peaks, at least for short-
53 term mates [12]. For long-term partnerships such as marriage, however, residual reproductive
54 value - the expected future reproductive output - becomes more pertinent [13]. In humans, this
55 trend is strengthened by the existence of reproductive senescence or menopause, i.e., the
56 permanent cessation of menstruation, associated with the ultimate cessation of child-bearing
57 potential. When reproductive and somatic senescence are disconnected, as they are in human
58 females, the residual reproductive value becomes independent of longevity.

59 Thus, in the presence of such a short temporal reproductive window, youth is an important
60 factor of women's attractiveness [14], as it signals a high residual reproductive value. For a
61 given age, the temporal reproductive window will vary according to the age at menopause,
62 which is variable both across and within populations [15-19]. If the future age at menopause
63 is somehow detectable in young adults, it should contribute substantially to mate choice and
64 thus influence female attractiveness. It is possible that previously identified components of
65 female attractiveness that have mostly been linked to immediate fertility are also informative
66 of female residual reproductive value. Alternatively, future age at menopause could be a
67 correlate of attractiveness that has not yet been identified.

68 In this study, we investigated whether residual reproductive value is related to the
69 attractiveness of women's faces. To understand how the residual reproductive value could be
70 facially detectable, all possible known components of facial attractiveness, including fertility

71 cues, were used as controlling variables. As menopause is heritable [16, 20-22], mother's age
72 at menopause was used as a proxy for the daughter's expected age of menopause.

73

74 **2. Materials and Methods**

75 **2.1 Ethics Statement.** The protocol used to recruit participants and collect data was approved
76 (#1226659) by the French National Committee of Information and Liberty (CNIL). For each
77 participant, the general purpose of the study was explained (“a study on the determinants of
78 mate choice”) and a written voluntary agreement was requested for a statistical use of data
79 (private information and photographs). Data were analysed anonymously.

80 **2.2 Stimuli.** Sixty eight Caucasian women between 25 and 35 years of age were recruited by
81 social networks and advertising in Montpellier, France. Volunteers were instructed to come to
82 the lab after collecting information about their mother's and (when possible) grandmothers'
83 age at menopause and without wearing any make-up. For each woman, the following
84 information was collected: date and place of birth for themselves, their parents and
85 grandparents; monthly income (divided into ten classes from less than 760€ to more than
86 4705€) for themselves and their parents; education level; and age at menopause for their
87 mother and grandmothers. A facial photograph was taken with the same digital still camera
88 (Canon EOS 20D) at a distance of 1 m using the same general settings. Each woman was
89 asked to have a neutral facial expression and to remove any glasses or earrings. All
90 photographs were electronically processed using Adobe Photoshop CS3 to normalise size
91 (photographs were aligned on eyes position, with a fixed distance between eyes and chin),
92 colour balance, contrast and luminosity (using the Photoshop auto-corrections tools). The
93 backgrounds were replaced by a uniform grey colour (see figure 1). Women were recorded
94 reading the French version of a standard text (“La bise et le soleil”) using a Tascam DR-07
95 MKII digital recorder. Across each recording, the fundamental frequency (F0, the acoustic
96 correlate of pitch) was measured using Praat software [23]. Two indexes of body condition
97 were measured: body mass index (BMI, the body mass divided by the square of the height),

98 and waist-to-hip ratio (WHR, the ratio between body circumference at the waist and the hips).
99 A compensation of 20€ was provided for the subjects' participation.

100 **2.3 Procedure.** A Delphi-based computer program was generated to present randomly drawn
101 pairs of photographs to 119 male raters (see figure 1). For each pair, the rater was instructed to
102 click on the photograph depicting the woman he found the most attractive. The position of the
103 photograph on the screen (left or right) was randomly ascribed. Each rater had 30 distinct
104 pairs of photographs to assess, corresponding to 60 different women. If the rater knew one of
105 the women he had to judge, the trial was removed. Also, the first pair seen by each participant
106 was not used for the analyses, because the task could require some habituation. Three pairs,
107 randomly chosen from among those previously viewed, were presented again at the end to
108 estimate judgement reliability. For each rater, the following information was collected: date
109 and place of birth, grandparents' origins, monthly income, occupation, house ownership,
110 taxability, education level, and sexual orientation.

111 **2.4 Morphological measurements.** Twenty-three points of interest were positioned on the
112 facial photograph of each woman [24-27] (see figure S1). To measure the facial asymmetry of
113 female participants, differences between 8 corresponding distances on each side of the face
114 were calculated for each participant. Each difference was weighted by the mean of the two
115 corresponding distances. A Principal Component Analysis (PCA) was performed on the
116 resulting four variables to obtain a new synthetic variable corresponding to an asymmetry
117 axis. The position of each woman along this axis represents her individual synthetic
118 asymmetry value. To assess facial femininity, 10 distances were computed from the same 23
119 points for all female subjects (for the whole method, see [24]). Similar measurements were
120 performed on facial photographs of a random sample of 68 men between 25 and 35 years of
121 age (derived from the male sample described in [25]). A linear discriminant analysis (LDA)
122 according to sex was performed on the male and female measurements, providing a synthetic
123 variable corresponding to a masculinity/femininity axis (see figure S2). The position of each

124 woman along this axis represents her individual femininity value. All morphological
125 measurements were performed using Image J version 1.43, and R version 3.0.1.

126 **2.5 Estimation of facial ageing.** A second Delphi-based computer program was generated to
127 present randomly drawn photographs to 107 raters (see figure S3). For each photograph, the
128 rater was instructed to estimate the age of the woman. Each rater had 20 distinct photographs
129 to assess. Three photographs, randomly chosen among those previously viewed, were
130 presented again at the end to estimate judgement reliability. For each rater, information about
131 sex and age was collected. For each woman, the difference between their real age and the
132 mean age given by the raters was calculated. This variable represents the facial ageing of the
133 women.

134 For the attractiveness and the facial ageing tests, volunteer raters were recruited in public
135 places in Montpellier, France and were unaware of the purpose of the study when assessing
136 the pairs of women. The general purpose of the study was explained to each participant and a
137 written agreement was requested for the use of their private information for academic
138 purposes.

139 **2.6 Statistical analyses.** Logistical regression was used to analyse raters' preferences. The
140 binary response variable corresponded to being chosen or not for the focal woman (arbitrarily
141 the woman presented at the left position) during the presentation of each pair. Women and
142 raters were considered random samples from a larger population of interest and were thus
143 random-effect variables. Therefore, generalised linear mixed models with binomial error
144 structure were used. For each choice made by a rater, the difference between the ages at
145 menopause of the focal and the non-focal woman's mothers was calculated. The value of this
146 difference was integrated into the model as the explanatory variable. For each variable known
147 to covary with facial attractiveness (facial femininity and asymmetry), the difference between
148 the focal woman and her competitor was calculated. The differences for variables 'facial
149 femininity' and 'facial asymmetry' were included as additional explanatory variables
150 (potentially mediating the relationship between expected age at menopause and facial

151 attractiveness). As raters' perception of women's age is too influenced by facial attractiveness,
152 facial ageing was not included in this model. BMI, WHR and F0, even if not possibly
153 mediating the relationship between expected age at menopause and facial attractiveness from
154 photographs, are linked to estrogens levels which covary with facial attractiveness. So the
155 differences between the two women for these 3 variables were also included as additional
156 explanatory variables. To control for potential confounding effects, the differences between
157 the focal and the non-focal woman's ages and socio-economic status (a PCA combination of
158 education level and the woman's and her parents' monthly incomes) were introduced into the
159 model. Because the subjects displayed a perceptible smile in some photographs, a qualitative
160 variable describing this aspect was also introduced. Variables concerning the raters'
161 characteristics were also included in the model as potential confounding effects. These
162 variables included: the rater's age and socio-economic status (a PCA combination of the
163 variables "monthly income", "occupation", "house ownership", "taxability", and "education
164 level"). For each parameter estimate, odds ratio (*OR*) and 95% confidence interval (*CI*) were
165 provided. Linear regression was used to analyse the mother's age at menopause (response
166 variable) according to the maternal grandmother's age at menopause (explanatory variable).
167 The "one-parent - one child" regression coefficient represents half the heritability (h^2) of the
168 trait [28]. Pearson correlations were used to analyse relationships between expected age at
169 menopause (estimated by mother's age at menopause) and each woman's measured trait:
170 facial femininity, asymmetry and ageing, BMI, WHR, F0, age, and socio-economic status. A
171 Pearson correlation was also used to analyse the relationship between facial attractiveness and
172 facial ageing. All statistical analyses were performed using R 3.0.1 software (R Core
173 Development Team).

174

175 **3. Results**

176 **3.1 Final sample.** A total of 97 women were sampled. Sixty eight Caucasian women whose
177 mother had a natural and known menopause were used for the attractiveness test (mean age =

178 28.4, age range: 25-35). A total of 156 male raters assessed the relative attractiveness of these
179 women. Only data from Caucasian and heterosexual raters were used for the analyses.
180 Assessments of unreliable raters (i.e., with more than one incorrect answer during the test of
181 judgement reliability) were removed. A total of 119 raters were retained in the final sample,
182 with a mean age of 36.3 (age range: 17-72). Each woman was observed, on average, by 101.1
183 raters (range: 93-108). For facial ageing estimation, a total of 136 raters assessed the age of
184 the 68 women. Assessments of unreliable raters (i.e., with a sum of absolute differences
185 between the first estimations and the corresponding repetitions, superior to 15) were removed.
186 A total of 107 raters (including 61 women) were retained in the final sample, with a mean age
187 of 35.1 (age range: 16-65). Each woman was observed, on average, by 31.2 raters (range: 24-
188 43).

189 **3.2 Attractiveness, menopause and fertility.** The variable expected age at menopause
190 (estimated by mother's age at menopause) had a significant positive effect on the probability
191 for a woman to be chosen as the most attractive ($OR = 1.040$, $CI = (1.015, 1.065)$, $P = 0.0013$,
192 see figure 2): Men tend to prefer women whose expected age at menopause is the latest.
193 Moreover, various other cues of reproductive potential had an effect on the probability of
194 being chosen (see table 1). There was a significant positive effect for the variable F0 ($OR =$
195 1.012 , $CI = (1.0074, 1.016)$, $P < 0.0001$), and a significant negative effect for facial
196 asymmetry ($OR = 0.87$, $CI = (0.79, 0.90)$, $P < 0.0001$): men tend to prefer the faces of women
197 who are more symmetric, and who have a higher-pitched voice. The variables femininity,
198 BMI and WHR had no significant effect on attractiveness ($P = 0.69$, $P = 0.44$ and $P = 0.066$
199 respectively). Women's age and smile demonstrated a significant effect on the probability of
200 being chosen: men preferred women who were younger ($OR = 0.98$, $CI = (0.95, 1.00)$, $P =$
201 0.056) and smiled more ($OR = 1.56$, $CI = (1.32, 1.91)$, $P < 0.0001$). There was no effect
202 observed for the socio-economic status of the woman ($P = 0.15$). The raters' age and socio-
203 economic level had no significant effect on their choices ($P = 0.82$ and $P = 0.91$ respectively).

204 **3.3 Heritability of age at menopause.** Among the 97 women, 42 completed information
205 about both their mother's and maternal grandmother's menopause. The mean age at
206 menopause was 51.0 (range: 42-58) for the mothers and 50.3 (range: 39-60) for the
207 grandmothers. The maternal grandmother's age at menopause had a significant effect on the
208 mother's age at menopause ($\beta = 0.274$, $P = 0.015$, see figure 3). This implies a heritability of
209 age at menopause from the maternal side of 27.4% ($SE = 0.11$) and thus an overall heritability
210 $h^2 \sim 55\%$ ($SE = 0.22$).

211 **3.4 Menopause and other women's features.** There was no significant correlation between
212 expected age at menopause and the fertility cues of facial femininity ($\rho = -0.077$, $P = 0.53$),
213 facial asymmetry ($\rho = -0.027$, $P = 0.83$), BMI ($\rho = -0.14$, $P = 0.25$), WHR ($\rho = -0.044$, $P =$
214 0.72) and F0 ($\rho = -0.96$, $P = 0.56$). Facial ageing was significantly correlated to attractiveness
215 ($\rho = -2.75$, $P = 0.0076$), but not to expected age at menopause ($\rho = -0.027$, $P = 0.34$). The
216 correlations between the expected age at menopause and the woman's age and between the
217 expected age at menopause and the socio-economic status were not significantly different
218 from zero ($\rho = 0.066$, $P = 0.59$; $\rho = 0.13$, $P = 0.28$, respectively).

219 **4. Discussion**

220 Here, we show that expected age at menopause is significantly related to the facial
221 attractiveness of young women. This result holds when variables potentially reflecting sex-
222 hormone exposure (facial femininity, voice pitch, and WHR), developmental stability (facial
223 symmetry), body condition (age and BMI), or socio-economic status are controlled.
224 Additionally, none of the other considered variables, including fertility cues and facial ageing,
225 were significantly correlated with the expected age at menopause. Thus, the expected age at
226 menopause seems to be linked to an independent facial information, which was not deducible
227 from previously documented components of facial attractiveness.

228 Results classically found in the literature were replicated in this study, suggesting that
229 this sample of young females is not different from those described elsewhere. For example,

230 facial symmetry and high voice pitch were positively correlated with facial attractiveness, as
231 in previous studies [3, 29-31]. Also, attractive faces were rated younger than their true age, as
232 in the study of Kwart [32]. Our sample provided a heritability estimate of the age at
233 menopause of 0.55, consistent with previous values ranging from 0.42 to 0.63 [16, 20-22].
234 Spurious significant results may sometimes arise following model simplification [33]. This
235 statistical bias is unlikely in this study, as all terms were kept and no model simplification was
236 performed. However, it is still possible that a confounding variable, which remains to be
237 identified, explains the link between expected age at menopause and facial attractiveness.

238 Men's preference for women signalling a late age at menopause (and thus a longer
239 temporal reproductive window) suggests that there is currently a selection towards a later
240 menopause, at least in Western societies, assuming that preferences reflect actual mate choice
241 for this trait, which remains to be established. Interestingly, a secular trend of increased
242 menopausal age has recently been observed [19, 34, 35]. This suggests that the social, familial
243 and cultural conditions found currently in Western societies are promoting selection towards a
244 later menopause in women. As a consequence, studies carried out in these societies are most
245 likely insufficient to test evolutionary hypotheses on the occurrence of female reproductive
246 senescence in the human lineage.

247 Somatic senescence, or ageing, is readily detectable in a face through wrinkles, skin
248 texture and coloration, etc. (for a review, see [36]). Those traits are specifically targeted by
249 cosmetic changes when a younger appearance is desirable. Facial traits correlated with
250 reproductive senescence have yet to be identified, and it remains to be determined whether
251 they can be, or are already, manipulated to increase attractiveness by signalling a later
252 menopause.

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263

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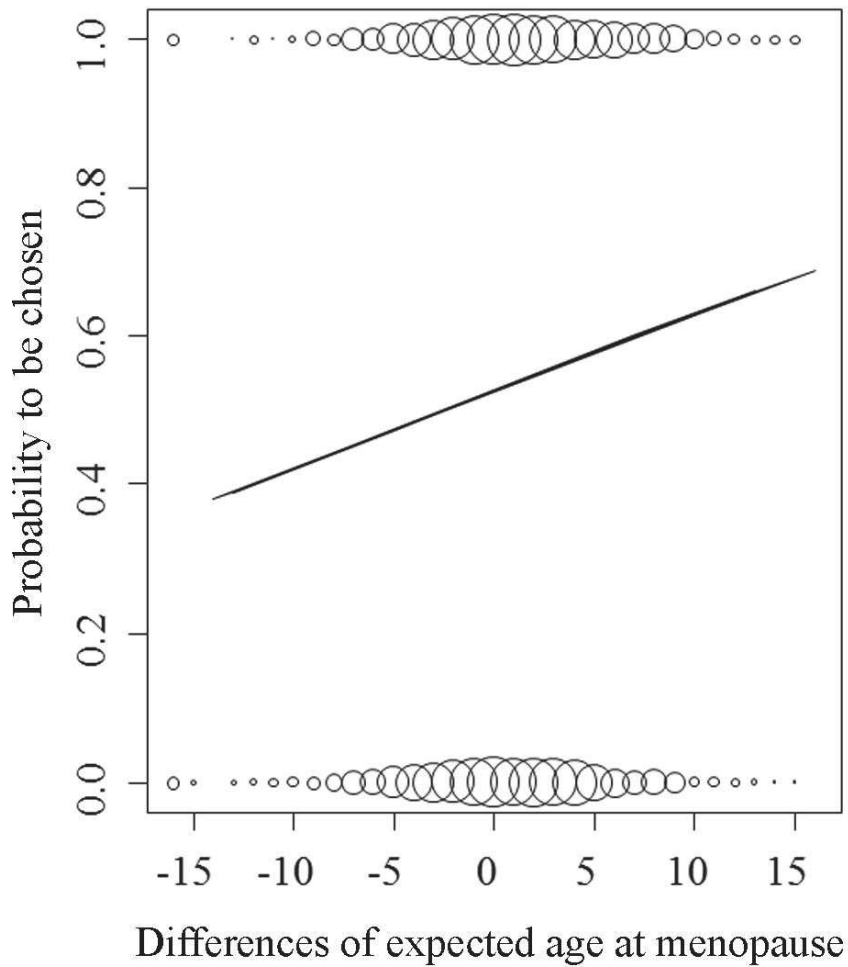
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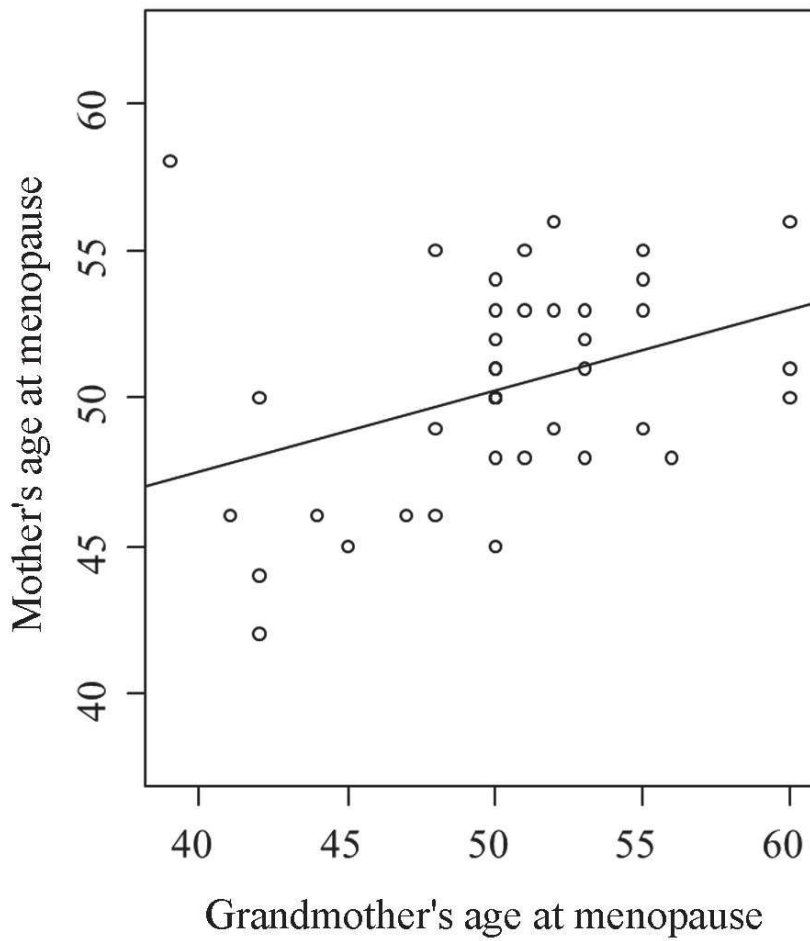
355 **Figure 1.** Example of screenshot during the evaluation of women's facial attractiveness by the
356 raters. For each pair of women, which was randomly chosen, the rater was instructed to click
357 on the photograph of the woman that he found the most attractive. Photographs reproduced
358 with permission.



359

360 **Figure 2.** Predicted probability to be chosen during the test of attractiveness, according to the
 361 difference in expected age at menopause between the focal and the non-focal women. Other
 362 variables of the model (facial femininity, facial asymmetry, BMI, WHR, F0, ages and socio-
 363 economic status of the woman and the rater), were set at their mean values. Circle areas are
 364 proportional to the number of choices made by the raters.

365



367

368 **Figure 3.** Relationship between age at menopause of mothers and maternal grandmothers.
 369 Plain line represents the linear regression with all points ($b = 0.27$, $P = 0.016$, corresponding
 370 to a heritability of age at menopause (h^2) = 0.55).

371

372 **Table 1.** Effects of the different variables on the probability to be chosen during the test of
 373 attractiveness. (Male raters had to choose the woman found to be the most attractive between
 374 two facial photographs). OR: odds ratio; CI: confidence interval.

375

Variable	OR	95% CI	P value
<i>(Intercept)</i>	1.12	(0.72, 1.74)	0.60
Mother's age at menopause*	1.04	(1.015, 1.065)	0.0013
<i>Fertility cues</i>			
Facial femininity*	0.98	(0.91, 1.065)	0.69
Facial asymmetry*	0.84	(0.79, 0.90)	< 0.0001
F0*	1.01	(1.007, 1.016)	< 0.0001
BMI*	0.99	(0.96, 1.02)	0.44
WHR *	5.95	(0.89, 39.67)	0.066
<i>Confounding variables</i>			
Age*	0.98	(0.95, 1.00)	0.056
Smile*	1.59	(1.32, 1.91)	< 0.0001
Socio-economic status*	0.93	(0.84, 1.027)	0.15
<i>Raters' characteristics</i>			
Age	0.99	(0.99, 1.01)	0.82
Socio-economic status	0.99	(0.83, 1.17)	0.91

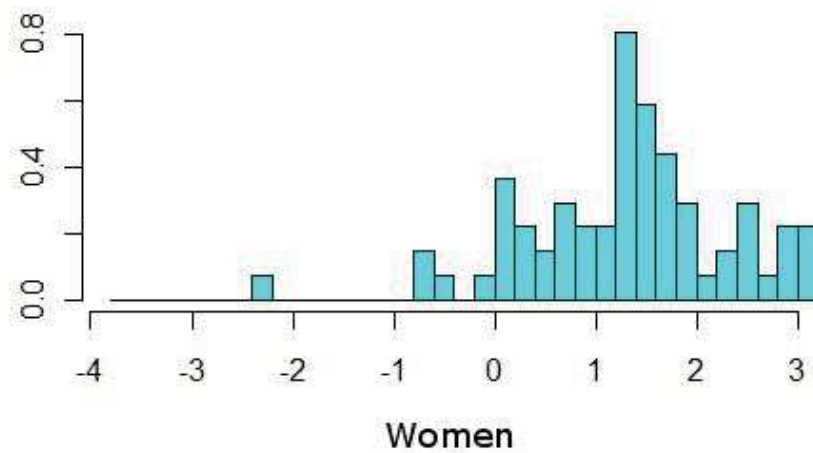
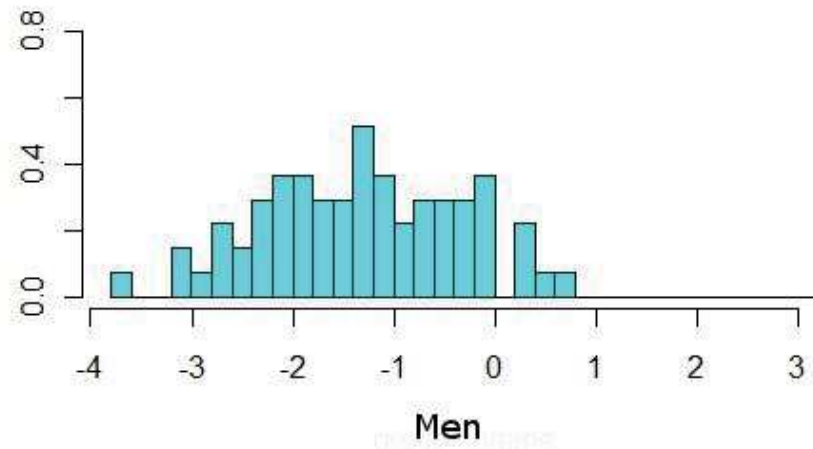
*For each variable, the difference between the two women presented was integrated in the model.

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377

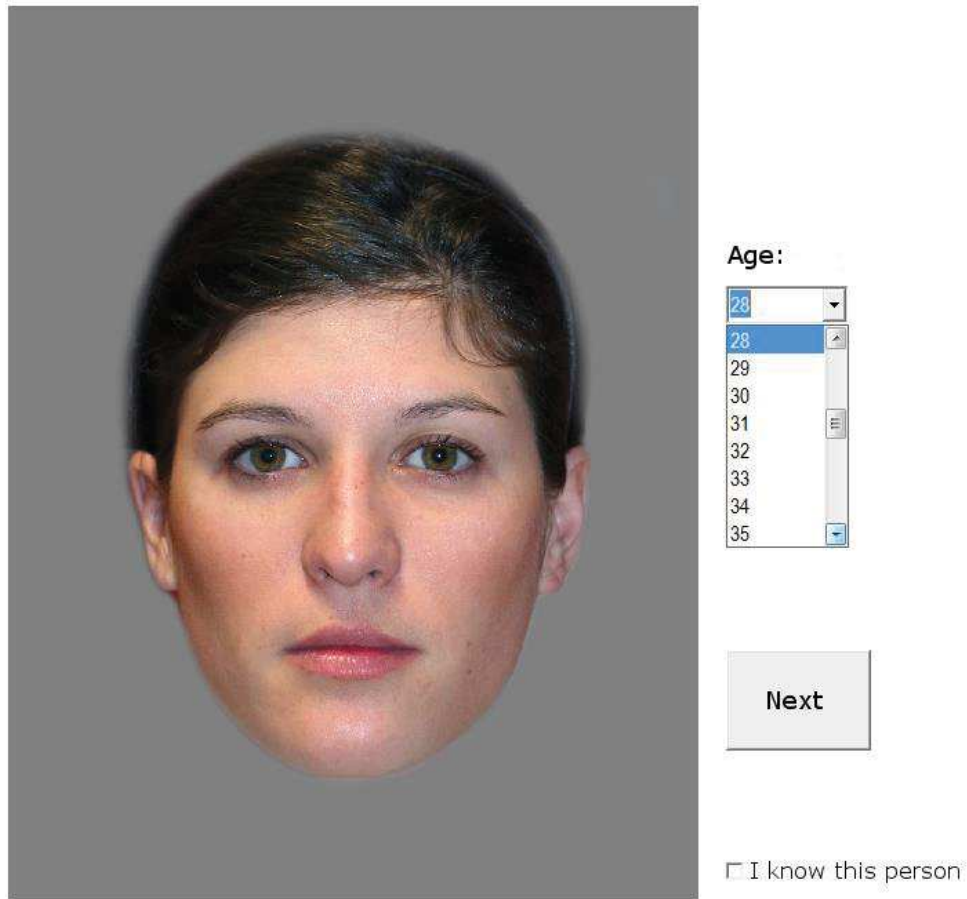
378 **Figure S1.** Twenty-three references points for measurement of asymmetry and femininity. For
 379 asymmetry, eight distances on each side of the face were considered: (2-3) vs. (4-5), (2-14) vs.
 380 (5-14), (15-8) vs. (16-9) and (3-17) vs. (4-17). For femininity/masculinity, 10 distances were
 381 computed see [24]: D1 (1-14), D2 (6-7), D3 (18-14), D4 $((20-21)+(22-23))/2$, D5 $((2-3)+(4-$
 382 $5))/2$, D6 (15-16), D7 (18-19), D8 (12-13), D9 (10-11) and D10 (1-19). Horizontal and
 383 vertical normalisations were performed: D4 and D7 were normalized with D1; D5, D6, D8
 384 and D9 with D2, and D3 with D10. Photograph reproduced with permission.



385

386 **Figure S2.** Result of the linear discriminant analysis (LDA) according to sex performed on
 387 the measurements of the 68 women and 68 men. The LDA provides a synthetic variable
 388 corresponding to a masculinity/femininity axis. The position of each woman along this axis
 389 represents her individual femininity value.

390



How old is she ?

391

392 **Figure S3.** Example of screenshot during the evaluation of women's age by the raters. The
393 rater was instructed to estimate the women's age. For each woman, the difference between
394 their real age and the mean age given by the raters was calculated. This variable represents the
395 facial ageing of the women. Photograph reproduced with permission.

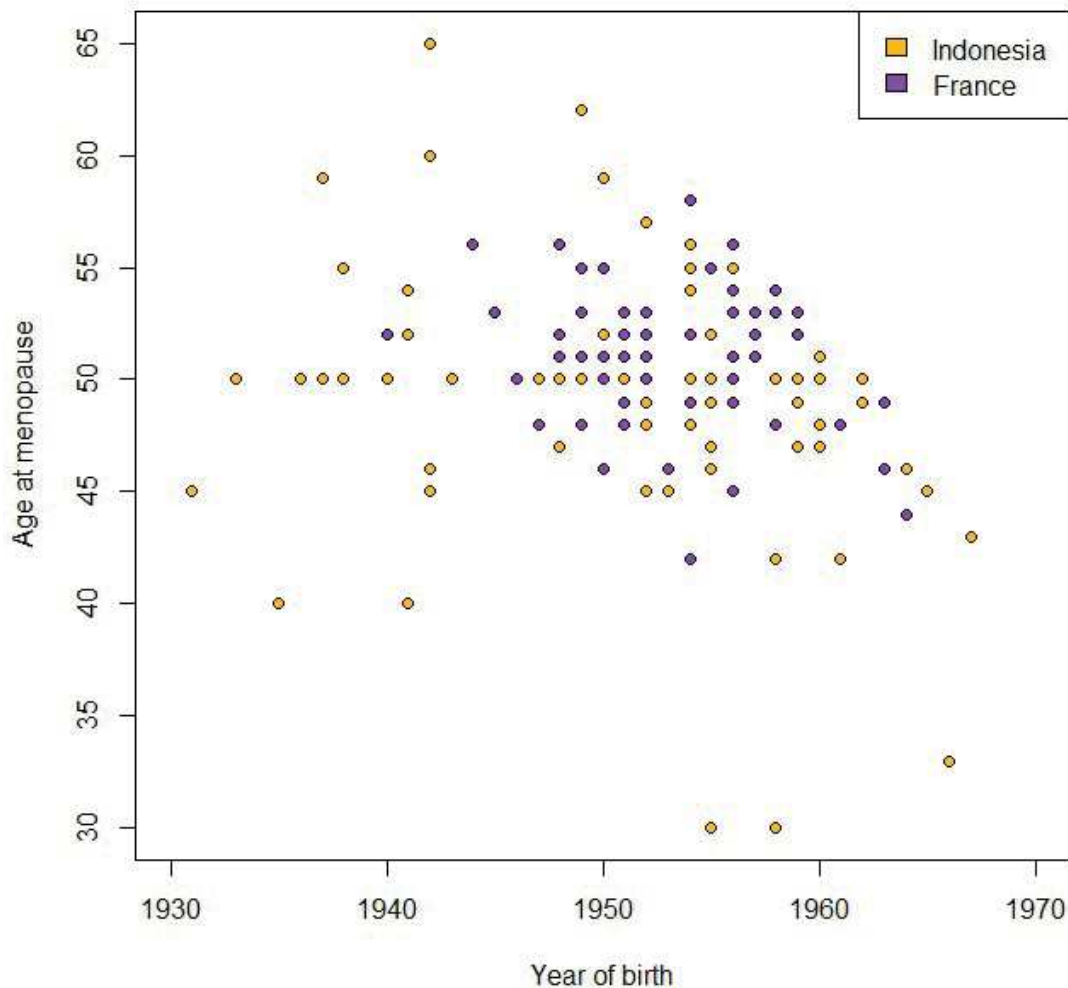
III. Les variations des préférences masculines

III.1. Variations géographiques (Article 3)

Nous avons mis en évidence l'existence d'un nouveau composant de l'attractivité féminine : le futur âge attendu à la ménopause. Nous avons cherché à savoir si cette préférence pour des femmes avec une plus longue période reproductive était limitée à notre échantillon Caucasien, ou s'il s'agissait d'un comportement plus global. Par ailleurs, une des hypothèses de l'apparition et de la maintenance de la ménopause dans l'espèce humaine suppose une population patrilinéaire (il s'agit de l'hypothèse du conflit reproducteur entre générations, n'existant que si les femmes dispersent et s'installent dans la famille de leur partenaire; Cant & Johnstone 2008). Nous avons donc choisi de réaliser une seconde étude dans une société aux conditions culturelles et environnementales différentes, qui de plus repose sur un système matrilineaire (les femmes restent dans leur famille d'origine) : les Minangkabau de Sumatra, en Indonésie.

Les résultats de cette étude montrent que dans cette population aussi, l'âge à la ménopause attendu est significativement relié à l'attractivité des jeunes femmes. Mais contrairement aux résultats de l'étude menée en France, ici l'âge à la ménopause attendu a un effet négatif sur la probabilité d'être choisie comme la jeune fille la plus attirante lors de la présentation des paires de photos : les hommes ont eu tendance à préférer les femmes dont le futur âge à la ménopause (estimé par celui de leur mère) était le plus faible. Ici

Encadré 6. Age à la ménopause en fonction du temps, en France et en Indonésie.



Age à la ménopause en fonction de l'année de naissance, pour l'étude réalisée en France (en violet, $N = 68$), et pour celle menée chez les Minangkabau en Indonésie (en jaune, $N = 73$).

D'après nos données, l'âge à la ménopause semble avancer légèrement chez les Minangkabau ($\beta = 0.13$, $P = 0.058$), mais pas en France ($P = 0.13$). De plus, en corrigeant pour l'année de naissance, on observe une différence significative de l'âge à la ménopause entre les deux pays ($\beta = 2.78$, $P = 0.0013$) : les femmes Minangkabau atteignent la ménopause plus tôt, en moyenne, que les Françaises.

aussi, plusieurs variables liées à la fertilité immédiate avaient un effet sur l'attractivité : les juges préféraient les femmes plus jeunes, ayant un visage plus symétrique et plus féminin, et un WHR plus faible. Comme pour l'échantillon français, il n'y avait aucune corrélation entre l'âge à la ménopause attendu et les différentes variables de fertilité immédiate ou d'attractivité (féminité et symétrie faciale, WHR, BMI).

ARTICLE 3

Women's attractiveness is linked to expected
age at menopause: A study on Minangkabau,
Sumatra, Indonesia

Jeanne Bovet, Rizaldi, Bambang Suryobroto, Valérie Durand, Michel Raymond

En préparation

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Women's attractiveness is linked to expected age at menopause:

A study on Minangkabau, Sumatra, Indonesia

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24 **Abstract**

25 Why some women have more attractive face than others has been the focus of many
26 studies. For short-term mating, males are expected to prefer females at the age of peak
27 fertility. In fact, facial fertility cues are linked to female attractiveness. For long-term
28 partnerships, a high residual reproductive value – the expected future reproductive output –
29 becomes more pertinent; thus, young age and late menopause are expected to be preferred.
30 In a first study, we have shown that expected age at menopause influences facial
31 attractiveness of French young women. As studies carried out in these societies are most
32 likely insufficient to test evolutionary hypotheses on the occurrence of female reproductive
33 senescence in the human lineage, the same experiment was carried out in Minangkabau
34 society of West Sumatra, in Indonesia. One of the evolutionary hypotheses on the evolution
35 of menopause (intergenerational reproductive conflict hypothesis) requires a patrilocal
36 system. As the Minangkabau have a matrilineal culture, age at menopause could have
37 different implications there. As age at menopause is heritable, we used the mother's age at
38 menopause as a proxy for the daughter's expected age of menopause. Contrary to the
39 results of the study carried in France, we found that men judged facial photographs of
40 women with an earlier expected age at menopause as more attractive than those of women
41 with a later expected age at menopause. This result holds when age and other components
42 of facial and non-facial attractiveness were controlled. Additionally, we found that the
43 expected age at menopause was not correlated with any of the other variables considered
44 (including fertility and developmental cues). This result confirms that expected age at
45 menopause is an independent component of women's facial attractiveness, but suggests
46 that the direction of men's preferences differ between France and Minangkabau
47 populations.

48 **Key words:** Mate choice, Facial attractiveness, Menopause, Matrilineal, Minangkabau

49 **Materials and Methods**

50 *Ethics Statement.* For each participant, the general purpose of the study was explained (“a
51 study on the determinants of mate choice”) and a written voluntary agreement was
52 requested for a statistical use of data (private information & photographs). Data were
53 analysed anonymously.

54

55 *Stimuli.* One hundred and fifty nine women (mean age: 46.99; age range: 13-100 years old)
56 were interviewed in the Minangkabau society of West Sumatra, in Indonesia. Interviews
57 were conducted in their native language by local researchers. For each woman, social,
58 economic and familial information was collected. Two indexes of body condition were
59 measured: body mass index (BMI, the volume height index), and waist-to-hip ratio (WHR,
60 the ratio between body circumference at the waist and the hips). A facial photograph was
61 taken taken with the same digital still camera (Canon EOS 20D) using the same general
62 settings. Each woman was asked to have a neutral facial expression and to remove any
63 glasses or earrings. Within these 159 women, we identified 28 mother-daughter pairs with
64 the mother postmenopausal and the daughter under 35 years old. Facial photographs of the
65 28 daughters were normalized for size, color balance, contrast and luminosity. The
66 backgrounds were replaced by a uniform grey color (see figure 1).

67

68 *Procedure.* To estimate women’s attractiveness, a Delphi-based computer program was
69 generated to present randomly drawn pairs of photographs to raters (see figure 1). For each
70 pair, the rater was instructed to click on the photograph depicting the woman he found the
71 most attractive. The position of the photograph on the screen (left or right) was randomly
72 ascribed. Each rater had 14 distinct pairs of photographs to assess, corresponding to the 28
73 daughters of the sample. The first pair seen by each participant was not used for the

74 analyses, because the task could require some habituation. Three pairs, randomly chosen
75 among those previously viewed, were presented again at the end to estimate judgement
76 reliability. For each rater, the following information was be collected: sex, date and place
77 of birth, and monthly income.

78

79 *Morphological measurements.* Twenty-three points of interest were positioned on the facial
80 photograph of each woman (Penton-Voak, Jones et al. 2001; Gangestad & Thornhill 2003;
81 Little, Jones et al. 2008). To measure the facial asymmetry of female participants,
82 differences between 8 corresponding distances on each side of the face were calculated for
83 each participant. Each difference was weighted by the mean of the two corresponding
84 distances. A Principal Component Analysis (PCA) was performed on the resulting four
85 variables to obtain a new synthetic variable corresponding to an asymmetry axis. The
86 position of each woman along this axis represents her individual synthetic asymmetry
87 value. To assess facial femininity, 10 distances were computed from the same 23 points for
88 all female subjects (for the whole method, see Gangestad & Thornhill 2003). Similar
89 measurements were performed on facial photographs of a random sample of 21 men from
90 the same population, between 25 and 35 years of age. A linear discriminant analysis (LDA)
91 according to sex was performed on the male and female measurements, providing a
92 synthetic variable corresponding to a masculinity/femininity axis. The position of each
93 woman along this axis represents her individual femininity value. All morphological
94 measurements were performed using Image J version 1.43, and R version 3.0.1.

95

96 *Statistical analyses.* Logistical regression was used to analyse raters' preferences. The
97 binary response variable corresponded to being chosen or not for the focal woman
98 (arbitrarily the woman presented at the left position) during the presentation of each pair.

99 Women and raters were considered random samples from a larger population of interest
100 and were thus random-effect variables. Therefore, generalised linear mixed models with
101 binomial error structure were used. For each choice made by a rater, the difference between
102 the ages at menopause of the focal and the non-focal woman's mothers was calculated. The
103 value of this difference was integrated into the model as the explanatory variable. For each
104 variable known to covary with facial attractiveness (facial femininity and asymmetry), the
105 difference between the focal woman and her competitor was calculated. The differences for
106 variables 'facial femininity' and 'facial asymmetry' were included as additional
107 explanatory variables (potentially mediating the relationship between expected age at
108 menopause and facial attractiveness). BMI and WHR, even if not possibly mediating the
109 relationship between expected age at menopause and facial attractiveness from
110 photographs, are linked to estrogens levels which covary with facial attractiveness. So the
111 differences between the two women for these 3 variables were also included as additional
112 explanatory variables. To control for potential confounding effects, the differences between
113 the focal and the non-focal woman's ages and socio-economic status (education level and
114 the woman's monthly income) were introduced into the model. Because the subjects
115 displayed a perceptible smile in some photographs, a qualitative variable describing this
116 aspect was also introduced. Variables concerning the raters' characteristics (age, sex and
117 monthly income) were also included in the model as potential confounding effects. Pearson
118 correlations were used to analyse relationships between expected age at menopause
119 (estimated by mother's age at menopause) and each woman's measured trait: facial
120 femininity, asymmetry and ageing, BMI, WHR, age, and socio-economic status. The
121 heritability of age at menopause couldn't be estimate in this sample, because only 5 post-
122 menopausal women knew the age at menopause of their mother. All statistical analyses
123 were performed using R 3.0.1 software (R Core Development Team).

124 **Results**

125 *Final sample.* Among the 159 women interviewed, 73 were post-menopausal. The mean
126 age at menopause in this sample was 48.89 years (range: 30-65 years), which is
127 significantly lower ($\beta = -2.78$; $P = 0.0013$) than mean age at menopause in the French
128 sample of our study 2 (mean age: 50.97; range: 42-58 years)(see Figure 2). Among the 73
129 post-menopausal women, 28 had a daughter under 35 who participated to our study (mean
130 age: 27.75; range: 16-35 years). A total of 116 raters assessed the relative attractiveness of
131 these 28 young women. Assessments of unreliable raters (i.e., with more than one incorrect
132 answer during the test of judgment reliability) were removed. A total of 110 raters (31 men
133 and 79 women) were retained in the final sample, with a mean age of 36.3 (age range: 17-
134 72).

135

136 *Attractiveness, menopause and fertility.* The variable expected age at menopause
137 (estimated by mother's age at menopause) had a significant negative effect on the
138 probability for a woman to be chosen as the most attractive ($\beta = -0.023$; $P = 0.019$): Men
139 tend to prefer women whose expected age at menopause is the earliest. Moreover, various
140 other cues of reproductive potential had an effect on the probability of being chosen (see
141 table 1). There was a significant positive effect for the variable femininity ($\beta = 0.32$;
142 $P < 0.0001$), and a significant negative effect for the variables facial asymmetry ($\beta = -0.12$;
143 $P = 0.013$) and WHR ($\beta = -3.48$; $P = 0.045$): men tend to prefer women more symmetric
144 and more feminine (according to both their face and WHR). The BMI had no significant
145 effect on facial attractiveness ($P = 0.33$). Women's age, smile and level of education
146 demonstrated a significant effect on the probability of being chosen: men preferred the
147 faces of women who were younger ($\beta = -0,068$; $P < 0.0001$), who smiled more ($\beta = 0.70$;
148 $P < 0.0001$), and who had a higher level of education ($\beta = 0.094$; $P = 0.0022$). There was

149 no effect observed for the woman's monthly income ($P = 0.62$). The raters' sex, age and
150 monthly income had no significant effect on their choices ($P = 0.65$; $P = 0.060$ and $P =$
151 0.47 respectively).

152

153 *Menopause and other women's features.* There was no significant correlation between
154 expected age at menopause and the fertility cues of facial femininity ($P = 0.55$), facial
155 asymmetry ($P = 0.53$), BMI ($P = 0.55$), and WHR ($P = 0.094$). The correlation between the
156 expected age at menopause and the level of education was not significantly different from
157 zero either ($P = 0.26$).

158

159 **Figures**



160 **Figure 1.** Example of screenshot during the evaluation of women's facial attractiveness by the
161 raters. For each pair of women, which was randomly chosen, the rater was instructed to click on
162 the photograph of the woman that he found the most attractive.

III.2. Variations temporelles (Article 4)

Le WHR est souvent pris en exemple comme critère universel de beauté (Singh 1993; Buss 2005; Singh 2006; Singh, Dixson et al. 2010; Singh & Singh 2011), mais certaines études mettent en doute l'invariabilité des préférences masculines concernant ce trait (Freese & Meland 2002; Pettijohn & Jungeberg 2004; Swami, Jones et al. 2009; Sorokowski & Sorokowska 2012). Or, si les tests de préférences masculines nous permettent d'identifier les composants de l'attractivité féminine d'aujourd'hui (et ce dans différentes régions géographiques), il est par contre plus difficile d'étudier les préférences des hommes dans le passé. Une possibilité est de prendre, comme reflet des préférences passées, des femmes ayant été choisies pour leur beauté à une époque donnée. Une série d'études a ainsi analysé les mensurations de modèles ayant posé pour *Playboy* (un magazine ayant un large public masculin), et des femmes ayant gagné des concours de beauté tels que *Miss America*. Cependant, il s'agit d'un passé relativement proche, car le magazine *Playboy* a été créé en 1953, et les concours de beauté datent des années 1920. Le but de cette étude était d'étendre l'analyse des préférences masculines à un passé plus ancien, grâce à des œuvres d'art. Il est souvent fait référence à certaines œuvres d'art plus ou moins anciennes, soit pour souligner un changement récent des critères de beauté féminine (Rubens est souvent cité, voir (Garner, Garfinkel et al. 1980; Swami, Gray et al. 2007)), soit comme preuve de l'invariabilité de ce critère de beauté (Singh 2002; Singh 2006). Mais, à notre connaissance, il n'existe aucune étude quantifiée se basant sur un grand nombre d'œuvres.

Nous avons donc récolté plus de 200 peintures et sculptures datant de la Grèce Antique à nos jours. Ces œuvres représentent des femmes considérées comme des symboles de beauté, puisque les sujets représentés sont des déesses de l'amour, de la beauté,

ou du plaisir telles que Vénus (ou Aphrodite), ou les Grâces. Les œuvres choisies montrent la silhouette des femmes (non cachée par des drapés ou vêtements), ce qui a permis à un grand panel de participants d'estimer la forme de leur corps. Le passage par des observateurs étaient un moyen d'obtenir une estimation plus juste de leur mensurations, car la variété des poses dans lesquelles ces femmes sont représentées rendait impossible une mesure standardisée faite directement sur les photos.

Les résultats de l'étude montrent que le WHR considéré comme idéal est resté relativement constant durant toute l'antiquité (de -500 à 400), autour d'une moyenne de 0,74. Ensuite, le WHR préféré a diminué du 15^{ème} jusqu'au 20^{ème} siècle, tout en restant cependant dans les limites de bonne santé et de fertilité (0,65-0,80). L'absence de données entre 400 et 1400 (due aux interdictions de l'Église Chrétienne sur la représentation artistique) rend difficile l'estimation de la date précise à laquelle a débuté cette diminution. Les données des femmes représentées dans les concours de beauté et dans le magazine *Playboy* montrent que cette diminution du WHR préféré a ralenti, et amorce même une remontée depuis les années 1960.

Cette étude remet donc en question l'invariabilité temporelle d'un WHR idéal, même si le WHR préféré reste relativement proche de la valeur de 0,7 fréquemment indiquée dans la bibliographie sur le sujet. Par ailleurs, contrairement à l'argument couramment avancé selon lequel les critères de beauté féminine aurait drastiquement changés avec l'apparition des médias de masse de ces dernières décennies, le changement des standards d'attractivité (du moins pour le WHR) semble plus ancien, puisque le WHR préféré commence à diminuer dès le XVe siècle.

Nous avons vu dans la partie I.3.i que les préférences pour la corpulence pouvaient

varier en fonction de l'environnement local, et il est possible que le même phénomène s'applique également au WHR. Par exemple, un WHR un peu plus élevé (donc moins féminin) pourrait être lié à une meilleure survie ou capacité à récupérer des ressources dans certains environnements hostiles, et pourrait être avantageux même si corrélé à une moins grande fertilité. Les changements du WHR idéal observés dans cette étude pourraient donc être expliqués par un changement de l'environnement dans les sociétés occidentales depuis le XVe siècle jusqu'à aujourd'hui. De fait, durant cette période, l'espérance de vie, la disponibilité des ressources et le produit intérieur brut ont augmenté dans ces sociétés (Roser 2014; Roser 2014; Roser 2014). Avec des conditions de vie devenant plus clémentes, avec plus de ressources et une meilleure santé générale, les préférences masculines pourraient avoir évolué vers un WHR plus faible (donc plus féminin), favorisant ainsi les indices de fertilité par rapport à d'autres indices utiles uniquement dans un environnement hostile.

ARTICLE 4

Preferred women's waist-to-hip ratio variation over
the last 2,500 years

Jeanne Bovet, Michel Raymond

Accepté dans Plos One

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Preferred Women’s Waist-to-Hip Ratio Variation over the Last 2,500 Years

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22 **Abstract**

23 The ratio between the body circumference at the waist and the hips (or WHR) is a secondary
24 sexual trait that is unique to humans and is well known to influence men's mate preferences.
25 Because a woman's WHR also provides information about her age, health and fertility, men's
26 preference concerning this physical feature may possibly be a cognitive adaptation selected in
27 the human lineage. However, it is unclear whether the preferred WHR in western countries
28 reflects a universal ideal, as geographic variation in non-western areas has been found, and
29 discordances about its temporal consistency remain in the literature. We analyzed the WHR of
30 women considered as ideally beautiful who were depicted in western artworks from 500 BCE to
31 the present. These vestiges of the past feminine ideal were then compared to more recent
32 symbols of beauty: *Playboy* models and winners of several *Miss* pageants from 1920 to 2014.
33 We found that the ideal WHR has changed over time in western societies: it was constant during
34 almost a millennium in antiquity (from 500 BCE to 400 CE) and has decreased from the 15th
35 century to the present. Then, based on *Playboy* models and *Miss* pageants winners, this
36 decrease appears to slow down or even reverse during the second half of the 20th century. The
37 universality of an ideal WHR is thus challenged, and historical changes in western societies
38 could have caused these variations in men's preferences. The potential adaptive explanations
39 for these results are discussed.

40

41

42

43 **Keywords:** women's attractiveness; men's preferences; waist-to-hip ratio; art

44 **Introduction**

45 Although women's attractiveness is considered complex and difficult to quantify, various
46 physical traits are now well known to influence men's mate choice. Among those traits, the
47 waist-to-hip ratio (WHR, the ratio between the body circumference at the waist and the hips),
48 which measures the distribution of body fat, has been the focus of extensive research.
49 Evolutionary theories of human mate selection contend that the WHR is an honest indicator of
50 fertility and is used by men to choose a mate likely to increase their reproductive success.
51 Consistent with this hypothesis, the distribution of body fat provides information about age,
52 health, fertility, and sexual behavior [1-7], and women with an hourglass shape (i.e., a low WHR)
53 are more attractive to men [2, 7-9]. One particular aspect of the literature has focused on the
54 universality of this preference for a low WHR. Several studies show a certain consistency
55 across populations in the preferences of men toward a low WHR [10-14], whereas a preference
56 for a relatively higher WHR has been observed in some other societies [15, 16]. However, this
57 apparent variability could result from the stimuli used, as other studies using different stimuli
58 found a preference for a low WHR [17, 18]. In fact, the stimuli used are not always adapted to
59 the local population, or do not control for the women's body mass [17, 19]. In addition, there is
60 no consensus concerning the consistency of WHR over time. Several studies have used
61 measurements of *Playboy* models and *Miss America* contestants, which are taken as
62 representative icons of western beauty standards. Here again, some studies underline the
63 remarkable consistency of the preferred WHR [20, 21], whereas others insist on the variability
64 of the ideal body shape over the last decades [22-25]. Nevertheless, studies based on data from
65 *Playboy* and *Miss* pageants concern the relatively recent past, with the oldest measurements
66 dating from the 1920s. For the more distant past, indications about physical preferences come
67 from artworks, such as paintings and sculptures. Although many references have been made to
68 ancient artworks, either to underscore the changing ideals of attractiveness in western societies
69 [22, 26], or to prove the invariability of the preferred WHR [3, 6, 27, 28] there is no published
70 quantitative study (to our knowledge) based on a large sample of artworks. This could be due to
71 the difficulty of obtaining measurements of women represented in artworks: it is complex to

72 objectively estimate the WHR of painted women with different postures or orientations. It is
73 easier for sculptures of nude women, although it could be difficult to have direct access to the
74 artworks scattered across museums. In addition, artwork has several purposes, and the depicted
75 women do not always represent the ideal woman body: it is thus important to consider only art
76 items specifically designed to represent attractive women. To our knowledge, this point has
77 never been considered.

78 This paper is divided into 3 studies. In the first study, we investigated the evolution of
79 WHR from 500 BCE to the present using artworks (painting and sculptures) representing
80 women usually considered as beautiful, such as Aphrodite or Venus. As the human brain has the
81 capacity to judge and very quickly and efficiently compare human bodies [29], even if not
82 normalized for characteristics such as the body posture, a large sample of observers was used to
83 estimate the WHR of women represented in artworks by comparing them to drawings of female
84 silhouettes. In the second study, we analyzed the evolution of WHR from 1920 to 2014 using
85 measurements of *Playboy* models and winners of several *Miss* pageants. In the third study, we
86 collapse these 2 datasets after a calibration step to find the best function describing the
87 evolution of the WHR according to time (from 500 BCE to 2014).

88

89 **Study 1**

90 **Materials and Methods**

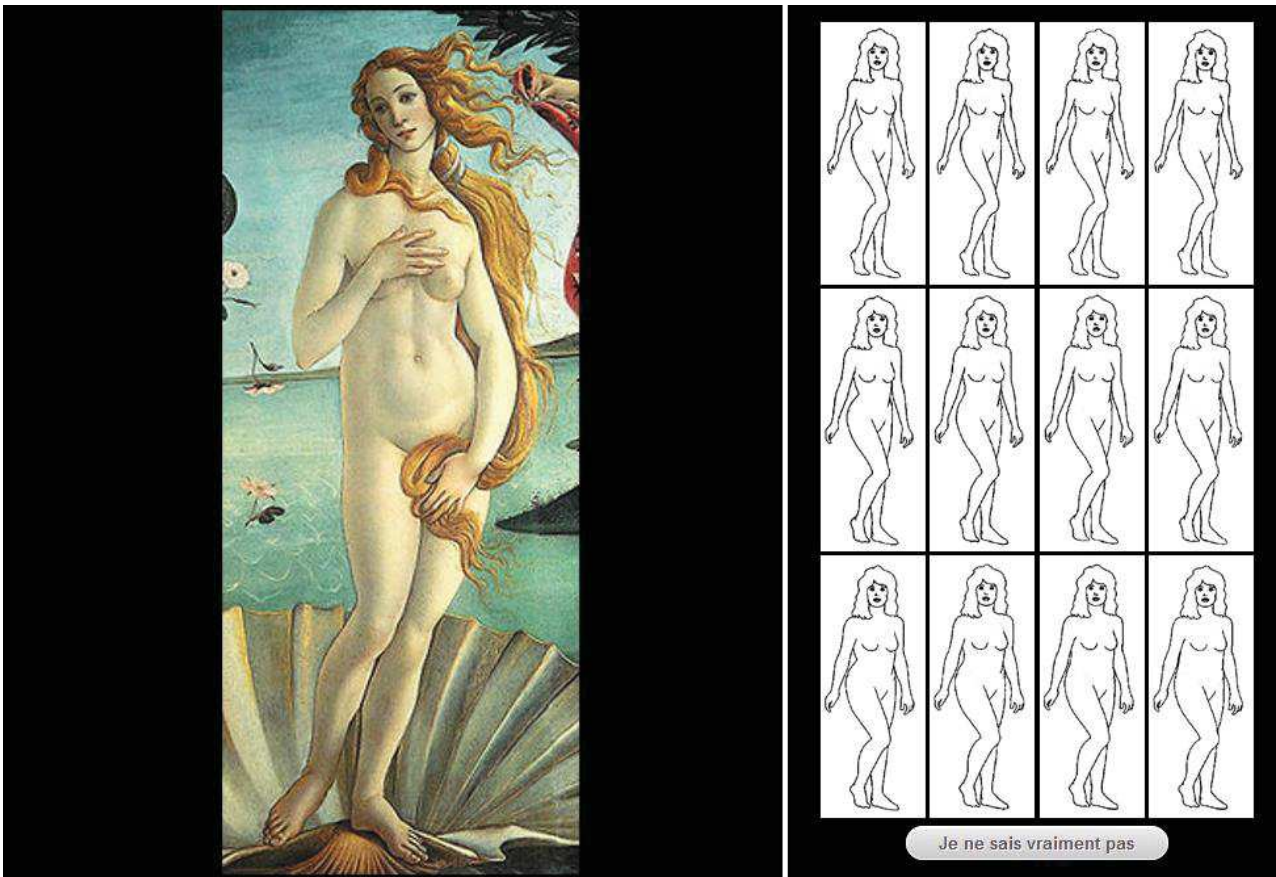
91 **Stimuli.**

92 216 artworks (160 paintings and 56 sculptures) representing women from 500 BCE to the
93 present were collected from various online open sources (mainly Wikipedia and art gallery
94 websites from various countries). One hundred and fifty of these artworks represented women
95 usually considered as beautiful, such as Aphrodite or Venus (Greek or Roman goddess of love,
96 beauty, pleasure, and procreation), Graces (Greek or Roman goddesses of charm, beauty, nature,
97 human creativity and fertility) and Psyche (a mythological young woman so beautiful that she
98 was compared to Venus), and 66 artworks represented women not specifically famous for their
99 beauty, such as Eve (according to the creation myth of Abrahamic religions, the first woman

100 created by God) and Susanna (a biblical Hebrew woman falsely accused by lecherous voyeurs).
101 In addition to the subject, the only selection criteria was that the selected painting or sculpture
102 should depict the woman at least partially naked, with a sufficient view allowing for the
103 evaluation of her silhouette. For each artwork, the following information was collected: date of
104 creation (divided into periods of 50 years), artist's name and birthplace, and subject depicted
105 (Aphrodite, Venus, Graces, Psyche, Eve or Susanna). The women's posture (standing, sitting or
106 lying) and orientation (front, back or profile) were recorded. All of the artists, and their
107 depictions, were Caucasian. If an artist had produced more than one version of the same subject,
108 the artwork allowing the easiest evaluation of the WHR (depending on the view, the woman's
109 posture, the quality of the picture, etc...) was chosen. The resulting sample is certainly not
110 comprehensive, although it is probably representative of what Wikipedia and art galleries
111 possess. Nude women have been represented in art during Classical Antiquity until the end of
112 the fourth century and were then almost completely absent from artwork during millennia due
113 to a ban from the Christian church [30, 31]. Nude women were represented again in artwork
114 during the Renaissance until today. Thus, the collected artworks were divided into an *antique*
115 period (from 500 BCE to 400 CE) and a *recent* period (from 1400 to 2014 CE).

116 *Procedure.* An online test was developed to randomly present artworks to raters. On the right
117 part of the screen, 12 drawn figures of women representing 3 different body weight categories
118 (underweight, normal weight and overweight) and 4 WHRs within each weight category were
119 displayed (the figures are from Singh [21], see figure 1). For each artwork, the rater had to click
120 on the figure that most closely resembled the woman depicted on the artwork. A given rater had
121 17 distinct artworks to assess, which were randomly chosen among the whole dataset. Then,
122 three artworks, which were randomly chosen among the 17 previously observed, were
123 presented again at the end to estimate judgment reliability. A judgment is considered as
124 unreliable if, for the same artwork, the second judgment differs from the first one of more than
125 one figure in each dimension (WHR or weight). Because the task could require some time to be
126 completely understood by the raters, the 4 first judgments of each rater were not included in the
127 analyses. Volunteer raters were unaware of the purpose of the study when assessing artworks.
128 Public advertisements were dispatched in local stores and social networks. These

129 advertisements contained the principle of the test (rating artworks), and a website address.
130 People went to the website on their own will if they wanted to participate. For each rater, only
131 sex, age and nationality were collected. This information could not allow a personal
132 identification (identifying information such as name or IP address were not collected). The
133 content of this experiment (an online evaluation of artworks), didn't required any specific
134 authorization from an ethics committee. Written consent was not required from the participants
135 for an online survey (their volunteer participation on the web site is equivalent to a tacit
136 consent). Moreover, participants could confirm their willingness to participate to our study
137 through a question displayed at the end of the online test (and only those that agreed where
138 considered for further analyses).



139

140 **Figure 1.** A typical screen shot during the evaluation of the women's silhouettes in the artworks by the participants in
 141 **Study 1.** An online test was developed to randomly present artworks to raters. On the right part of the screen, 12 drawn figures
 142 of women were displayed, representing 3 different weight categories and 4 WHRs within each weight category (from Singh
 143 [21]). For each artwork, the rater had to click on the figure that most closely resembled the woman depicted on the artwork
 144 according to the rater. A given rater had 17 distinct artworks to assess. Three artworks, which were randomly chosen among
 145 those previously observed, were presented again at the end to estimate judgment reliability.

146

147 **Statistical analysis.**

148 Because participants had to compare two-dimensional pictures, we directly measured the
 149 apparent WHR on the 2D-drawn figures from Singh [21]. These WHR measures were
 150 associated with each choice made by raters, and a mean estimated WHR was calculated for each
 151 woman. Linear regressions were used to analyze the mean estimated WHR of each woman
 152 (numeric variable from 0.70 to 0.92). In the first model, we compared women's mean WHR for
 153 *antique* and *recent* artworks (binary variable). Then, within each period, we analyzed the effect

154 of the date of the artworks' creation (continuous variable) on women's WHR. In all models, the
155 type of artwork (painting or sculpture), woman's posture (standing, sitting or lying) and
156 orientation (front, back or profile) were integrated as confounding variables. A variable
157 "category" (*High attractiveness* if the depicted woman was Venus, Aphrodite, Graces or Psyche,
158 and *Control* if she was Eve or Susanna) was also integrated. As each rater judged only a small
159 fraction of the total number of artwork ($13/216 \approx 6\%$), each woman was observed by a specific
160 sample of raters. For each artwork, the raters' mean age and sex ratio were calculated and
161 integrated into the models as confounding variables. To control for potential habituation effects,
162 the mean place of appearance during the test was calculated for each artwork and also
163 integrated into the model as a confounding variable. As each rater judged a random and unique
164 sample of artworks, the expected number of artworks in common to two raters was small (lower
165 than 1), limiting the capacity to compute the inter-rater reliability. Tentatively, Krippendorff's
166 alpha [32] was used to estimate this value. All statistical analyses were performed using R
167 2.11.1 (R Core Development Team).

168 **Results**

169 **Descriptive statistics.**

170 2,164 people responded to the online test. The assessments from non-westerners (according to
171 their declared nationality) and unreliable raters (i.e., raters who did not finish the test or with
172 one or more incorrect answers during the test of judgment reliability) were removed. A total of
173 1,437 raters were retained in the final sample (mean age 37.4, age range: 18-90, 923 females).
174 Each artwork was evaluated by an average of 75.02 raters (range: 50-118). The inter-rater
175 reliability, estimated by Krippendorff's alpha, was equal to 0.26.

176 **Artworks WHR.**

177 The women's mean estimated WHR varied from 0.715 to 0.883. There was no significant
178 difference between the WHRs of *antique* and *recent* artworks (mean WHR = 0.798 for both,
179 $P = 0.19$). Within the *antique* artworks, there was no significant effect of the date of creation on
180 the WHR ($P = 0.40$, see table 1). There was no effect of the artwork type (painting or sculpture),
181 woman's posture (standing, sitting or lying) or orientation (face, back or profile) ($P > 0.4$ for all

182 variables). Within the *recent* artworks, there was a significant linear and quadratic effect of the
183 date of creation on the WHR (linear effect: $\beta = 0.13$, $P = 0.0020$; quadratic effect: $\beta = -0.0041$,
184 $P = 0.0011$): the artworks' WHR decreased over time during the *recent* period (1400-2000).
185 There was a significant difference between *the high attractiveness* and the *control* women: *high*
186 *attractiveness* women had a lower WHR than the *control* women ($\beta = -0.014$, $P = 0.010$). There
187 was a significant effect of the woman's posture: sitting women were rated as having a higher
188 WHR than standing or lying women ($\beta = 0.012$, $P = 0.031$). There was no effect of the artwork
189 type ($P = 0.060$) or woman's orientation ($P > 0.1$). In all the models, the effects of the sample of
190 raters' characteristics (sex ratio and mean age) and the artwork mean place of appearance
191 during the test were not significant ($P > 0.2$).

192 **Table 1. Results for study 1.** Linear regressions were used to analyze the mean estimated WHR of each woman (numeric
 193 variable from 0.70 to 0.92). Within each period, we analyzed the effect of the date of the artworks' creation on women's WHR.
 194 In all models, the type of artwork (painting or sculpture), woman's posture (standing, sitting or lying) and orientation (front,
 195 back or profile) were integrated as confounding variables. A variable "category" (*High attractiveness* if the depicted woman
 196 was Venus, Aphrodite, Graces or Psyche, and *Control* if she was Eve or Susanna) was also integrated. For each artwork, the
 197 raters' mean age and sex ratio were calculated and integrated into the models as confounding variables. To control for potential
 198 habituation effects, the mean place of appearance during the test was calculated for each artwork and also integrated into the
 199 model as a confounding variable.

200

Variable (value)	Estimate	P-value
Antique artworks		
Intercept	0.88	< 0.001
Date of creation	-0.0017	0.40
Artwork type (painting)	0.020	0.44
Woman's posture (sitting)	0.011	0.56
(lying)	-0.018	0.41
Woman's orientation (back)	-0.019	0.47
(profile)	-0.00016	0.99
Raters' sex ratio	-0.077	0.47
Raters' mean age	0.0013	0.64
Mean place of appearance	-0.0082	0.46
Recent artworks		
Intercept	-0.46	0.25
Date of creation	0.13	0.0020
(Date of creation) ²	-0.0041	0.0011
Artwork type (painting)	0.012	0.060
Woman's posture (sitting)	0.012	0.031
(lying)	-0.0074	0.26
Woman's orientation (back)	-0.013	0.14
(profile)	0.0083	0.10
Category (high attractiveness)	-0.014	0.010
Raters' sex ratio	0.048	0.25
Raters' mean age	0.00070	0.52
Mean place of appearance	0.0041	0.42

201

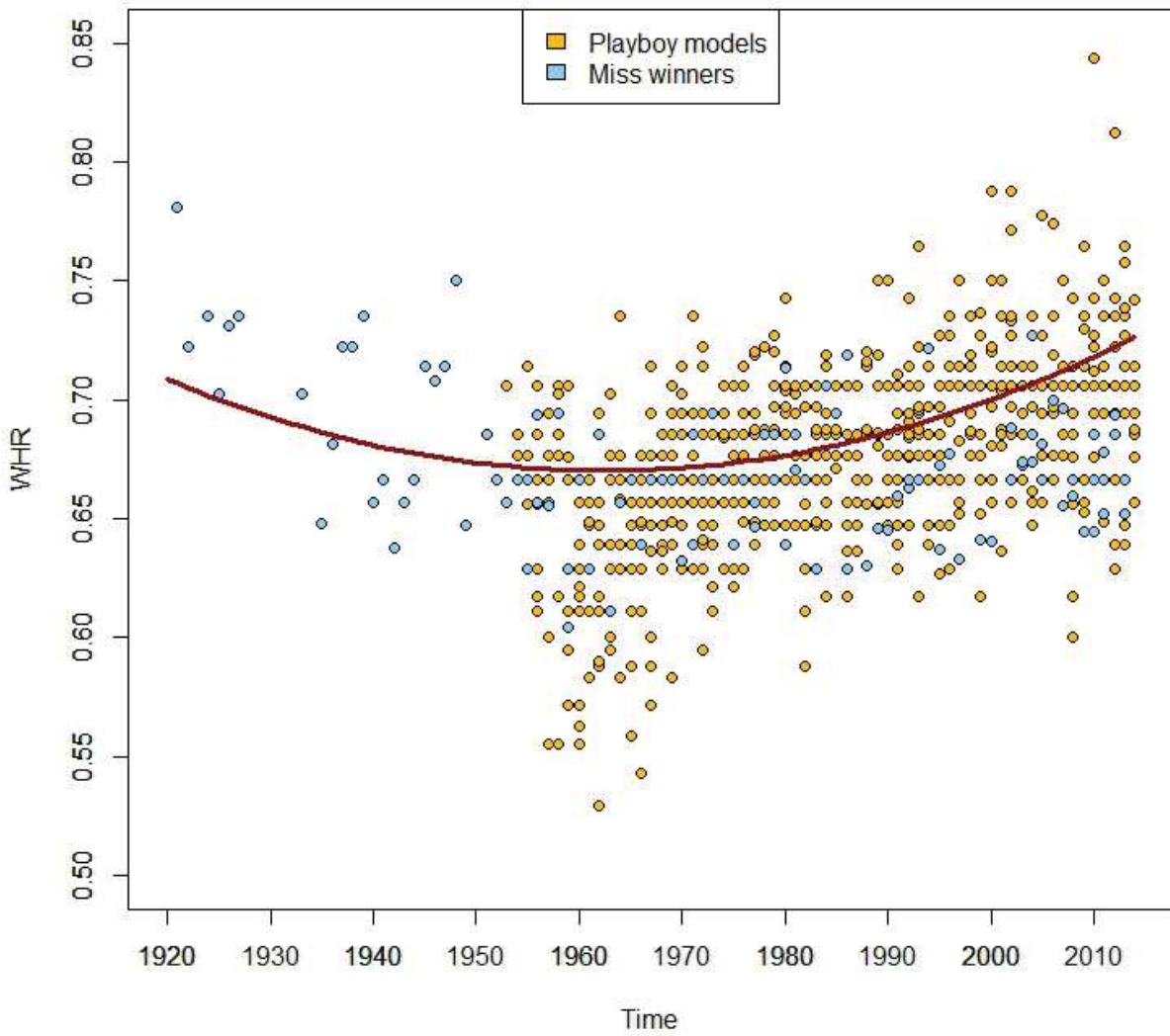
202 **Study 2**

203 **Materials and Methods**

204 Data on the WHR of *Playboy* centerfold models from 1953 to 2001 are available in Freese [24]
205 and the *Playboy* corporation website. We collected the measurements of centerfold models
206 from 2001 to July 2014 from the *Playboy* corporation website and Wikipedia. Data for the *Miss*
207 *America* winners from 1921 to 1986 (when the pageant stopped collecting this information) are
208 available in [24]. When available online, we also collected measurements of the *Miss Universe*,
209 *Miss World* and *Miss Earth* pageant winners. Linear regressions were used to study WHR
210 according to time.

211 **Results**

212 During the period from 1921-2014, the *Playboy* models and *Miss* pageants winners' WHR
213 ranged from 0.529 (for Mickey Winters, appeared in *Playboy* centerfold of Sept. 1962, 45.7
214 cm/86.3 cm) to 0.844 (for Ashley Hobbs, appeared in *Playboy* centerfold of Dec. 2010, 68.5
215 cm/81.2 cm), with a mean of 0.677. The data were better fit by a model when including a
216 quadratic term: the women's WHR had a curvilinear relationship with time ($\beta = -0.083$ and $\beta =$
217 2.12×10^{-5} for time and time², respectively, $P < 0.0001$, see figure 2).
218



219

220 Figure 2. WHR values for *Playboy* centerfold models (in yellow) and winners of 4 *Miss* pageants (*Miss America*, *Miss*

221 *World*, *Miss Earth* and *Miss Universe*, in blue) by time of magazine appearance or victory. The data were fit by a linear

222 regression that includes a quadratic term (in red).

223

224

225 **Study 3**

226 **Materials and Methods**

227 We created a new dataset including the WHRs of artworks, *Playboy* centerfold models and the
228 winners of *Miss* pageants.

229 **Calibration of artworks WHR.**

230 In study 1, we demonstrated the effect of the artwork type and woman's posture and orientation
231 on the participants' estimation of the WHR. The estimated WHRs were thus normalized to
232 make them correspond to a front view standing sculpture. To estimate the validity of the
233 participants' visual estimation of WHR, we directly measured the WHR of 13 sculptures of
234 standing women (11 *high attractiveness* and 2 *controls*) located in public places and museums
235 (the *Musée des Moulages* in Montpellier and the *Musée Archéologique* in Marseille). Then, for
236 each one of the 13 sculptures, we compared the "real WHR" to the mean WHR estimated by the
237 participants. The mean ratio between the real and estimated WHRs was used to calibrate all the
238 WHRs estimated by the participants.

239 **Parameterization and likelihood.**

240 According to study 1 and 2, the WHR of artworks was constant during the *antique* period (from
241 500 BCE to 400 CE) and decreased during the *recent* period (from 1400 to 2014). Study 2
242 showed that the *Playboy* models and *Miss* winners' WHR had a curvilinear relationship with
243 time. Thus, the evolution of the WHR according to time T on the whole dataset was modeled as
244 follows:

245 - during the *antique* period: $\text{WHR} = M_0$

246 where M_0 is the mean corrected WHR during the *antique* period

247 - during the *recent* period: $\text{WHR} = f(T)$

248 where $f(T)$ described the change of WHR according to time in the *recent* period, which
249 include artworks after 1400, the *Playboy* models and winners of *Miss* pageants.

250 Various forms have been explored for this function, notably:

- 251 A. $f(T) = \alpha + \beta T$
- 252 B. $f(T) = \alpha + \beta T + \gamma T^2$
- 253 C. $f(T) = \alpha + \beta T + \gamma T^2 + \delta T^3$
- 254 D. $f(T) = \alpha - e^{\beta T - \gamma}$

255 The likelihood of sampling the WHR observed in our dataset at date i (WHR_i) is as follows:

256 $L_1 = -\sum_i (WHR_i - M_0)^2$ for the *antique* period

257 $L_2 = -\sum_i (WHR_i - f(i))^2$ for the *recent* period

258 And the global likelihood over the two periods is as follows:

259 $L = L_1 + L_2$

260 Maximization of the likelihood function was performed using the optimization method of Byrd
 261 et al. [33], which uses a limited-memory modification of the quasi Newton algorithm. For each
 262 parameter set, 100 runs were performed, each starting with a random set of initial values to
 263 increase the chances of finding the true maximum. All statistical analyses were performed using
 264 R 2.11.1 (R Core Development Team).

265 **Results**

266 **Calibration of artworks WHR.**

267 The mean ratio between the 13 WHRs directly measured and the WHRs estimated for the same
 268 sculptures was 1.079 (range 1.018-1.221): on average, participants overestimated sculptures'
 269 WHR by 7.9%. Once corrected for the artwork type, women's posture and orientation, and
 270 participants' overestimation, the artworks' WHR varied from 0.655 (*The Awakening of Psyche*
 271 by Seignac, 1904) to 0.801 (*Susanna and the Elders* by Pontius, 17th century), with a mean of
 272 0.733.

273 **Model selection.**

274 For the full dataset including artworks, *Miss* pageants winners and *Playboy* models, the best
 275 model was A, with an AIC of 8.89 (see figure 3). Models B, D (displaying the same AIC of
 276 10.97), and C (AIC = 12.91) were rejected. The retained parameterization was therefore:

277

$WHR = 0.74$ during the *antique* period,

278 and

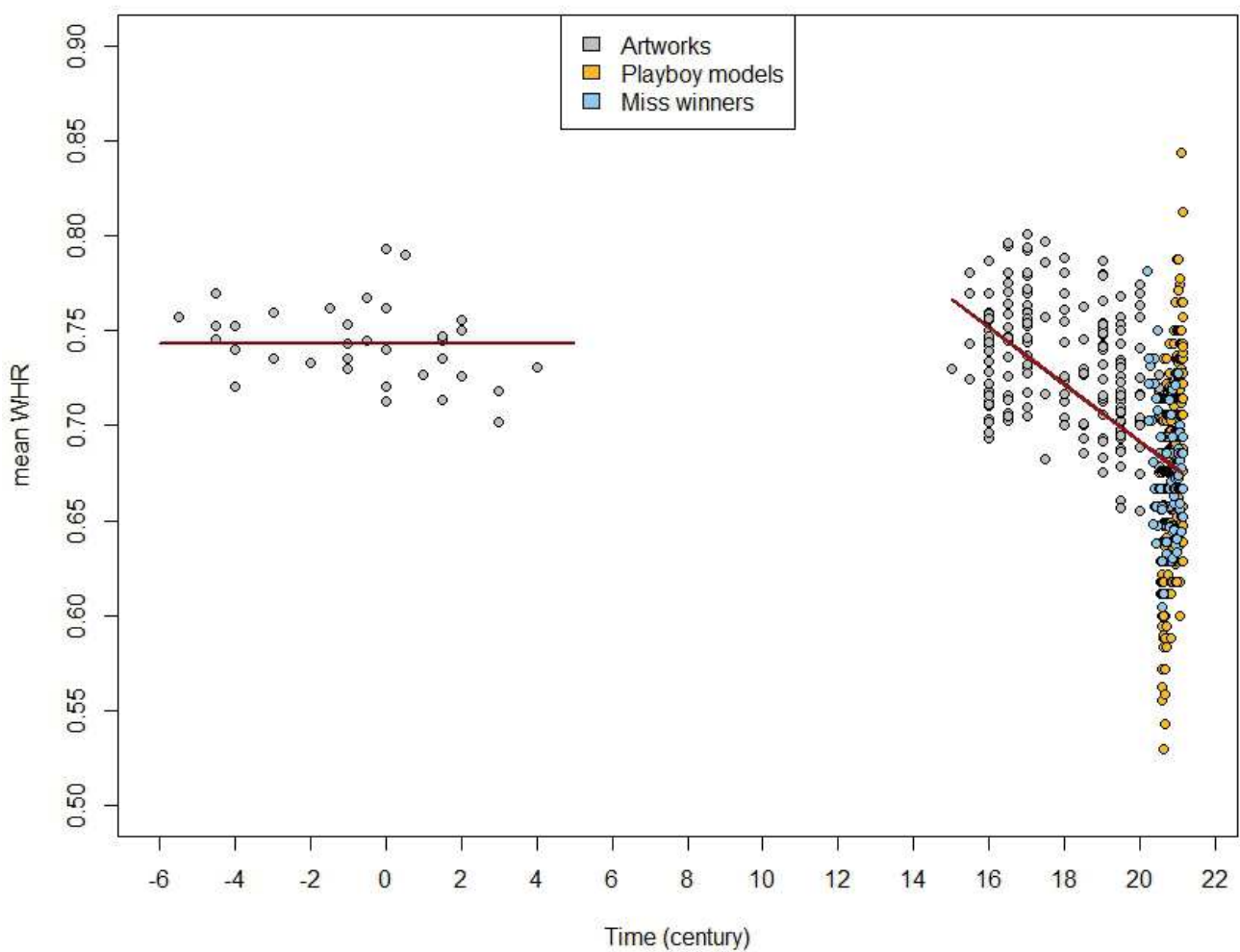
$WHR = 0.99 - 0.015 \times T$ during the *recent* period,

279 with T in century units, varying from 15 to 20.14. Thus, the WHR of women considered as

280 beautiful was constant during the *antique* period, and then, after a period with no nude women

281 depicted, the preferred WHR decreased from the 15-16th centuries until the present.

282



283 **Figure 3. Plot of WHR values for artworks (in gray), *Playboy* centerfold models (in yellow) and winners of *Miss***

284 **pageants (in blue) according to time.** The best model parameterization was as follows: $WHR = 0.74$ during the *antique* period

285 and $WHR = 0.99 - 0.015 * T$ during the *recent* period (in red).

286

287 **Discussion**

288 This is the first study to analyze men’s preferences on a broad time scale, with a large
289 number of artworks. By choosing artworks representing Greek or Roman goddesses (study 1),
290 we restricted the data to western societies. This choice permitted controlling for the artists’
291 willingness to represent the most beautiful women, which is often harder to prove for ancient
292 artworks from other cultures. Likewise, the so-called “palaeolithic Venus” figurines were not
293 included in our study because the intended representation remains unknown (see [34, 35] for the
294 variety of possible interpretations, spanning from goddess to dolls to symbols of fertility and
295 female power). The fact that, in our study, the represented goddess of beauty (*High*
296 *attractiveness* type) had a lower WHR than other women, such as Eve or Suzanna (*control* type),
297 underlines the importance of knowing the meaning of the artwork before their interpretation.

298 We showed that men’s preference for women’s WHR was remarkably constant from
299 500 BCE to 400 CE, with a mean WHR of 0.74. Then, the WHR considered as ideal decreased
300 from ca 1400 to the present, with a mean WHR of 0.68 for the beginning of the 21st century.
301 Due to the lack of data between 400 and 1400 (due to a ban from the Christian church to depict
302 nude women in art [30, 31], it is difficult to infer exactly when this decrease began and if other
303 variations occurred during this millennium gap.

304 Even if during the whole period considered here the preferred WHR remained close to
305 the value of 0.7 usually indicated as the ideal WHR in literature (mean for artworks in our study:
306 0.73) and remained within the normal and fertile range of feminine WHR (range for artworks in
307 our study: 0.65-0.80, normal range of western women: 0.67-0.80 [36]), there was a significant
308 change of men’s preferences during the last 500 years. This result shows that, contrary to the
309 assertion that the preference for WHR is universal and temporally invariant [3, 6, 21, 36], the
310 preferred WHR has changed over time. Moreover, in contrast with the common claim that the
311 ideal shape for women has dramatically changed in the last 20-50 years with the occurrence of
312 mass media, the shift of the beauty standards (at least for the WHR) seems to be older, as the
313 preferred WHR began to decrease since the 15th century.

314 According to evolutionary theory, men should prefer a female body shape that signals a
315 mate's high potential to contribute to his reproductive success. However, the usefulness of
316 attention to different signals of mate quality may vary depending on the environment, selecting
317 for facultative preferences that respond to environmental variation [37]. In this way, men's
318 preference for women's BMI vary considerably among populations [16, 38-41], with
319 low-resource men preferring a significantly heavier partner than high-resource men [42]. Some
320 studies suggest that a similar link between environment and men's preferences might exist for
321 the WHR, with men that live in harsher environments preferring a higher WHR [15, 16].
322 However, this could be an artifact related to the applied methodology, as other studies found a
323 preference for a low WHR in these societies [17, 18]. Moreover, men's facial femininity
324 preferences correlate positively with the health of the nation [43]. As femininity is associated
325 with lower ratings of dominance [44], this suggests that in harsher environments men prefer
326 cues to resource acquisition and holding potential over high fecundity [43]. The men's changing
327 preferences concerning the WHR in our study could thus be explained by a change of
328 environment in western societies during the period 1400-2000 [25]. In fact, during this period,
329 the life expectancy, food availability and gross domestic product (GDP) increased in western
330 populations [45-47]. Thus, with an environment becoming relatively more clement, with higher
331 resources and better health, men's preferences could have evolved toward a lower – thus a more
332 feminine – WHR, favoring cues of fecundity over resource acquisition and holding potential.
333 However, the majority of artworks were produced by relatively wealthy artists for extremely
334 wealthy aristocrats, which reduce the potential role of resources availability on preferences
335 variation.

336 Similarly, the remarkable consistency of the WHR represented in artworks during the
337 antique period (500 BCE - 400 CE) could be linked to the relative consistency of the
338 environment concerning health and resources in the society. However, the similarity of the
339 women represented during this period may be amplified by the fact that artwork imitation was
340 more widespread then, e.g., many Roman statues are Greek copies. This was controlled in this
341 study as much as possible, as statues known to be a copy of an older model were not considered.
342 Nevertheless, it cannot be excluded that widespread artwork imitation at this time, or the

343 restricted number of artworks that remained from this period (e.g., none of the paintings from
344 the Antique Greece have survived), contributes to the apparent stability of the ideal WHR.

345 The WHR of only *Playboy* models and *Miss* pageant winners (study 2) first decreased
346 and then increased since the 1960s. It is possible that some change in western society, which
347 remains to be identified, has induced this new trend. Interestingly, social inequalities have
348 followed a similar trend during the 20th century, with an initial decrease reflecting an evolution
349 toward more equalities, and then from the seventies, with an increase toward more wealth
350 inequalities [48]. Nevertheless, this phenomenon takes place on a small time frame (~50 years),
351 and it is difficult to compare to the general trend observed over half a millennium. Moreover,
352 this type of fluctuation may have occurred before but was not detected here due to the scale of
353 our sampling.

354 Alternatively, it has been proposed that the variation of the preferred WHR could result
355 from a another phenomenon: males may possess psychological adaptations that generate a
356 preference depending of the perceived local distribution of WHR in the population, this
357 perceived distribution being a function of the normal female range to which a man is exposed to
358 [49]. A change of the preferred WHR is thus expected when the perceived mean or range of
359 WHR in the population varies. The recent increase in women's average WHR in western
360 populations [50, 51] could explain the increase in the ideal WHR since the 1960s. Indirect
361 evidence suggest that the mean WHR has changed since the 15th century, for example during
362 the demographic transition (the number of pregnancies affects WHR), and more generally when
363 there was a change in a factor affecting the WHR, such as diet or parasite loads. Population data
364 on WHRs before the 1960s are required to further evaluate this hypothesis.

365 It is also possible that the women depicted in the present sample of artworks are not a
366 perfect indicator of men's preferences at a given time. The choice of the artworks
367 (representations of goddess of beauty) allows us to be relatively confident concerning the
368 artists' objective. But the ideal of beauty of the artists (or their buyers) may not be representative
369 of the preferences of the rest of the population. Similarly, while the physical appearance of the
370 *Miss* pageant winners and the models of *Playboys* is appreciated by the pageants audience and

371 the magazine readership, it nonetheless remains necessary to establish their validity as ideals for
372 a broader public.

373 The current medical recommendation for good health is a WHR below 0.85 for women
374 [52]. After calibration, no woman in our study showed a WHR higher than 0.85 (maximum of
375 0.844, see Study 2). Do the variations within the healthy range of WHR observed here still
376 correspond to fitness differences? The relationship between WHR and fertility is probably
377 continuous, suggesting that a variation (even slight) of WHR translates in a corresponding
378 variation of expected fertility. In fact, a 0.1 unit increase in WHR led to a 30% decrease in
379 probability of conception through artificial insemination [53]. Furthermore, even small
380 variations of WHR (<0.05) are detected by men and influence women's attractiveness [54, 55].
381 It suggests that the variation of the ideal WHR observed in our study - even within a relatively
382 narrow range (0.529-0.844) - could be adaptive.

383 In this study, we demonstrated that the WHR of women considered as symbols of beauty
384 did not vary during the antiquity period (500 BCE - 400 CE) and decreased since (at least) the
385 15th century in western societies. A closer analysis of *Playboy* models and *Miss* pageant
386 winners' measurements from 1920 to 2014 revealed a reduction, or even a reversion, of this
387 WHR decrease. The universality of one preferred WHR is thus challenged, and the evolution of
388 men's preferences could be linked to demographic, economic, health or social changes in
389 western societies, which are older than the mass media growth of the 20th century.

390 Our work shows the necessity to conduct more historical comparisons, which might
391 provide a novel and interesting extension of existing cross-cultural studies about attractiveness
392 [56, 57]. The cognitions and motivation of our ancestors are enshrined in art, which thus
393 comprises a rich data source for cross-generational studies.

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401

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529 **Supporting Information Legend**

530 **Table S1. Artworks used in this study.** This table presents, for each artwork, its title, author and date of creation, the identity
531 of the woman depicted, her posture and her orientation. The uncorrected WHRs correspond to the women's mean WHRs
532 estimated by the participants by comparing them to the drawn figures. The corrected WHRs correspond to the estimated WHRs
533 normalized for the type of artwork, the woman's posture and orientation, and for the raters' estimation bias.

Artworks	Artist	Century	Subject	Type	Posture	Orientation	Uncorrected WHR	Corrected WHR
The three Graces	Anonymous	-5.5	Grace	sculpture	standing	front	0.810	0.757
Aphrodite of Syracus	Praxitele	-4.5	Venus	sculpture	standing	front	0.806	0.753
Aphrodite of Cnidus	Praxitele	-4.5	Venus	sculpture	standing	front	0.798	0.746
Venus of the Capitol	Praxitele	-4.5	Venus	sculpture	standing	front	0.823	0.769
Aphrodite of Braschi	Praxitele	-4	Aphrodite	sculpture	standing	front	0.771	0.721
Aphrodite of Cnidus	Praxitele	-4	Aphrodite	sculpture	standing	mean	0.791	0.740
Venus of Arles	Praxitele	-4	Aphrodite	sculpture	standing	front	0.805	0.753
Crouching Venus	Anonymous	-3	Aphrodite	sculpture	sitting	profile	0.804	0.736
Aphrodite with a dolphin	Anonymous	-3	Aphrodite	sculpture	standing	mean	0.813	0.760
Aphrodite of Amisos	Anonymous	-2	Aphrodite	sculpture	lying	front	0.784	0.733
Venus de Milo	Anonymous	-1.5	Venus	sculpture	standing	mean	0.815	0.762
Medici Venus	Anonymous	-1	Aphrodite	sculpture	standing	mean	0.787	0.736
Medici Venus	Anonymous	-1	Aphrodite	sculpture	standing	front	0.806	0.754
Aphrodite	Antistios	-1	Aphrodite	sculpture	standing	front	0.781	0.730
Aphrodite	Diphilos	-1	Aphrodite	sculpture	standing	front	0.795	0.743
Aphrodite of Soli	Anonymous	-0.5	Venus	sculpture	standing	front	0.821	0.767
Aphrodite of Menophantos	Menophantos	-0.5	Venus	sculpture	standing	front	0.797	0.745
Aphrodite	Anonymous	0	Venus	sculpture	standing	mean	0.849	0.793
Aphrodite	Anonymous	0	Venus	sculpture	standing	mean	0.816	0.762
The Toilet of Venus	Anonymous	0	Aphrodite	sculpture	standing	mean	0.792	0.740
Aphrodite of Artemonos	Artemonos	0	Aphrodite	sculpture	sitting	front	0.788	0.721
Aphrodite of Cnidus	Diphilos	0	Aphrodite	sculpture	standing	front	0.763	0.713
Aphrodite and Eros	Molas	0.5	Aphrodite	sculpture	standing	front	0.845	0.790
Venus anadyomene	Anonymous	1	Venus	painting	lying	front	0.791	0.727
Crouching Venus	Anonymous	1.5	Aphrodite	sculpture	sitting	front	0.814	0.745
Aphrodite	Anonymous	1.5	Venus	sculpture	standing	mean	0.763	0.714
Venus of Arles	Anonymous	1.5	Venus	sculpture	standing	back	0.767	0.735
Venus of Amiens	Velazquez	1.5	Venus	sculpture	standing	front	0.799	0.747
Crouching Venus	Anonymous	2	Aphrodite	sculpture	sitting	profile	0.794	0.726
Crouching Venus	Anonymous	2	Aphrodite	sculpture	sitting	profile	0.825	0.755
Venus of Esquilin	Anonymous	2	Venus	sculpture	standing	mean	0.803	0.751
Aphrodite with a turtle	Anonymous	3	Venus	sculpture	standing	front	0.751	0.702

The Birth of Venus	Anonymous	3	Venus	painting	lying	front	0.782	0.718
Venus	Anonymous	4	Venus	painting	sitting	profile	0.813	0.731
Adam and Eve	Masolino	15	Eve	painting	standing	front	0.795	0.730
The Birth of Venus	Botticelli	15.5	Venus	painting	standing	front	0.789	0.724
Primavera	Botticelli	15.5	Grace	painting	standing	back	0.830	0.781
Adam and Eve	Cleve	15.5	Eve	painting	standing	front	0.809	0.743
Venus	Credi	15.5	Venus	painting	standing	front	0.837	0.770
Venus and Cupid with a Satyr	Allegri	16	Venus	painting	lying	profile	0.813	0.747
Aphrodite of Modesty	Anonymous	16	Venus	sculpture	standing	front	0.773	0.722
The three Graces	Baldung	16	Grace	painting	standing	front	0.765	0.702
Venus and Cupid	Baldung	16	Venus	painting	standing	front	0.755	0.693
Adam and Eve	Baldung	16	Eve	painting	standing	front	0.786	0.722
Venus, Cupid, Folly and Time	Bronzino	16	Venus	painting	sitting	front	0.799	0.718
Adam and Eve	Coxie	16	Eve	painting	standing	front	0.823	0.757
The three Graces	Cranach	16	Grace	painting	standing	front	0.774	0.711
Venus callipyge	Cranach	16	Venus	painting	standing	profile	0.793	0.728
Adam and Eve	Cranash	16	Eve	painting	standing	profile	0.793	0.729
Venus	Cranash	16	Venus	painting	standing	profile	0.776	0.713
Venus and Cupid	da Pontormo	16	Venus	painting	lying	front	0.856	0.787
Judgment of Paris	di Benvenuto	16	Venus	painting	standing	front	0.811	0.745
Adam and Eve	Durer	16	Eve	painting	standing	front	0.816	0.750
Adam and Eve	Durer	16	Eve	painting	standing	front	0.810	0.744
Venus frustrated	Fiorentino	16	Venus	painting	standing	front	0.810	0.744
Adam and Eve	Gossaert	16	Eve	painting	standing	front	0.813	0.747
Venus of Urbino	le Titien	16	Venus	painting	lying	profile	0.826	0.760
Venus anadyomene	le Titien	16	Venus	painting	standing	profile	0.856	0.787
Adam and Eve	Leyden	16	Eve	painting	standing	front	0.838	0.770
Susanna and the Elders	Mazzucchelli	16	Susanna	painting	standing	profile	0.825	0.759
Adam and Eve	Michelangelo	16	Eve	painting	sitting	profile	0.825	0.742
Venus and Cupid at Vulcan's Forge	Penni	16	Venus	painting	standing	front	0.780	0.716
Adam and Eve	Raphael	16	Eve	painting	standing	front	0.799	0.734
The three Graces	Raphael	16	Grace	painting	standing	front	0.822	0.755
Adam and Eve	Robbia	16	Eve	sculpture	standing	front	0.791	0.739

Cupid and Psyche	Romano	16	Psyche	painting	sitting	profile	0.792	0.711
Adam and Eve	Scorel	16	Eve	painting	standing	front	0.759	0.696
Venus and Cupid	Scorel	16	Venus	painting	sitting	front	0.784	0.704
Susanna and the Elders	Allori	16.5	Susanna	painting	sitting	profile	0.827	0.745
Venus and Cupid	Allori	16.5	Venus	painting	lying	front	0.791	0.726
Judgment of Paris	Bertoja	16.5	Venus	painting	standing	profile	0.818	0.752
Adam and Eve	Broeuck	16.5	Eve	sculpture	standing	profile	0.766	0.716
Venus and Adonis	Cambiaso	16.5	Venus	painting	standing	front	0.838	0.771
Venus and Cupid	De Backer	16.5	Venus	painting	standing	front	0.818	0.752
Psyche	De Vries	16.5	Psyche	sculpture	standing	front	0.752	0.703
Susanna and the Elders	Giuseppe	16.5	Susanna	painting	standing	front	0.812	0.746
Venus and Cupid	Limosin	16.5	Venus	painting	lying	front	0.769	0.706
Susanna and the Elders	Metsys	16.5	Susanna	painting	sitting	front	0.797	0.716
Susanna and the Elders	Palma	16.5	Susanna	painting	sitting	profile	0.818	0.736
Susanna and the Elders	Reymond	16.5	Susanna	painting	sitting	profile	0.860	0.775
Adam and Eve	Rubens	16.5	Eve	painting	standing	front	0.768	0.705
Venus and Cupid	Sustris	16.5	Venus	painting	lying	profile	0.825	0.758
Susanna and the Elders	Tintoret	16.5	Susanna	painting	sitting	profile	0.881	0.795
Adam and Eve	Tiziano	16.5	Eve	painting	standing	front	0.813	0.747
Black Venus	van der Schardt	16.5	Venus	sculpture	standing	front	0.835	0.780
Mars et Venus reunis par cupidon	Veronese	16.5	Venus	painting	standing	front	0.866	0.797
The three Graces	Von Aachen	16.5	Grace	painting	standing	front	0.777	0.713
Judgment of Paris	von Aachen	16.5	Venus	painting	standing	front	0.831	0.764
Susanna and the Elders	Blanchard	17	Susanna	painting	sitting	front	0.854	0.770
Vénus et les Grâces surprises par un mortel	Blanchard	17	Venus	painting	lying	front	0.810	0.744
Susanna and the Elders	Burg	17	Susanna	painting	sitting	front	0.814	0.732
Susanna and the Elders	Chauveau	17	Susanna	painting	sitting	front	0.879	0.793
Sleeping Venus	Gentileschi	17	Venus	painting	lying	profile	0.781	0.717
Susanna and the Elders	Gentileschi	17	Susanna	painting	sitting	front	0.785	0.705
Venus after her bath	Giambologna	17	Venus	sculpture	standing	profile	0.782	0.730
Susanna and the Elders	Goltzius	17	Susanna	painting	lying	front	0.847	0.779
Venus and Adonis	Goltzius	17	Venus	painting	sitting	front	0.790	0.710
Susanna and the Elders	Honthorst	17	Susanna	painting	standing	profile	0.863	0.793

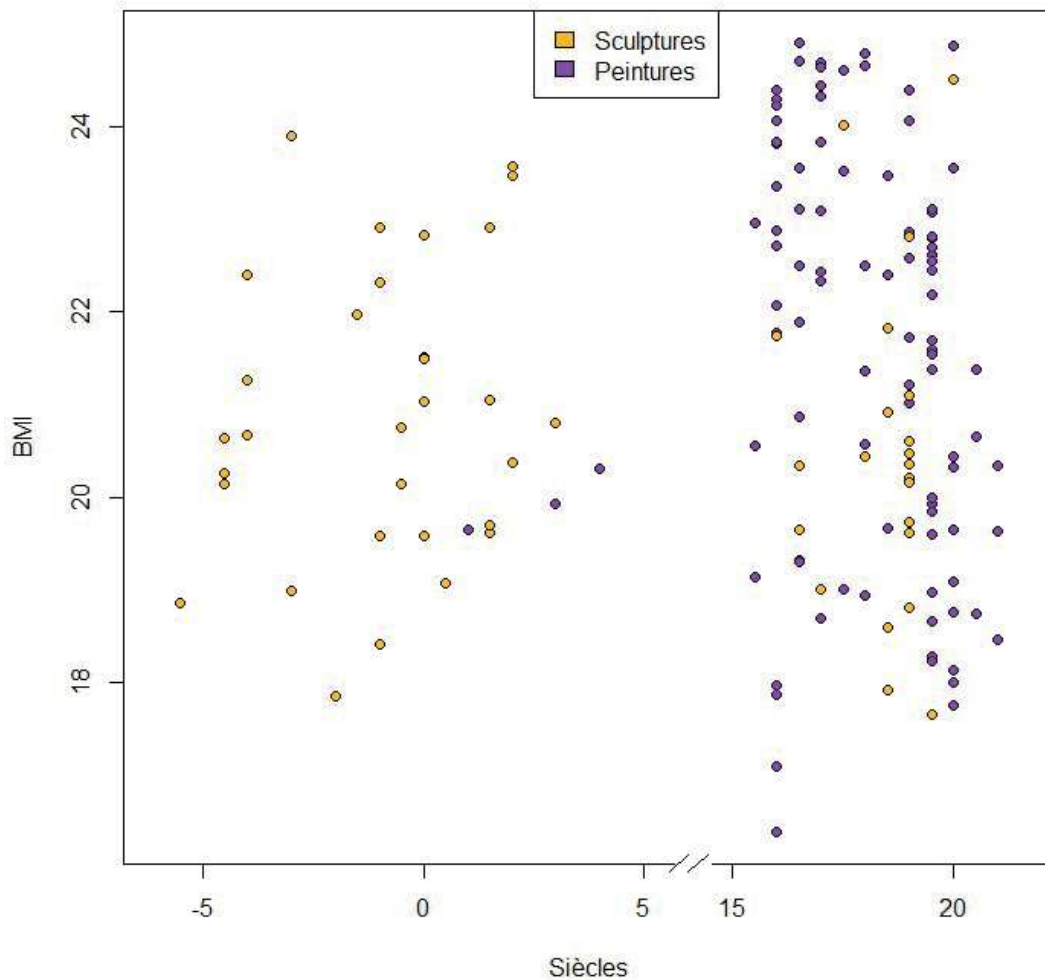
Adam and Eve	Paggi	17	Eve	painting	sitting	profile	0.829	0.746
Susanna and the Elders	Pontius	17	Susanna	painting	standing	profile	0.870	0.801
Venus and Mars	Poussin	17	Venus	painting	lying	profile	0.796	0.731
Susanna and the Elders	Rembrandt	17	Susanna	painting	sitting	profile	0.819	0.737
Reclining Venus with Cupid	Reni	17	Psyche	painting	lying	front	0.792	0.728
Susanna and the Elders	Reni	17	Susanna	painting	sitting	profile	0.840	0.756
Judgment of Paris	Rubens	17	Venus	painting	standing	front	0.830	0.763
Susanna and the Elders	Rubens	17	Susanna	painting	sitting	front	0.866	0.781
The three Graces	Rubens	17	Grace	painting	standing	back	0.820	0.772
Susanna and the Elders	Stanzione	17	Susanna	painting	sitting	front	0.838	0.754
Susanna and the Elders	Stella	17	Susanna	painting	sitting	profile	0.843	0.759
Cupid and Psyche	van Dyck	17	Psyche	painting	lying	front	0.827	0.760
Venus asks Vulcan to cast arms for her son Aeneas	van Dyck	17	Venus	painting	standing	front	0.871	0.801
Venus, Adonis and Cupid	van Ravesteyn	17	Venus	painting	sitting	profile	0.848	0.764
Adam and Eve	Zampieri	17	Eve	painting	sitting	front	0.836	0.753
Crouching Venus	Coysevox	17.5	Venus	sculpture	sitting	profile	0.827	0.757
Mars and Venus in the Forge of Vulcan	Giordano	17.5	Venus	painting	lying	front	0.780	0.717
Venus punishing Psyche	Giordano	17.5	Psyche	painting	standing	front	0.855	0.786
Susanna and the Elders	Jordaens	17.5	Susanna	painting	sitting	front	0.883	0.797
The Toilet of Venus	Vargas	17.5	Venus	painting	lying	back	0.724	0.682
A Triumph of Venus	Boucher	18	Venus	painting	sitting	profile	0.826	0.744
Abandoned Psyche	Coypel	18	Psyche	painting	sitting	profile	0.785	0.705
Susanna and the Elders	Coypel	18	Susanna	painting	sitting	front	0.806	0.724
Susanna and the Elders	La Fosse	18	Susanna	painting	sitting	profile	0.854	0.769
Venus and Nymphs Bath	Lagrenée	18	Venus	painting	standing	back	0.757	0.713
Venus	Pigalle	18	Venus	sculpture	sitting	front	0.831	0.761
Susanna and the Elders	Pittoni	18	Susanna	painting	sitting	profile	0.839	0.755
Venus and Mars	Pittoni	18	Venus	painting	sitting	profile	0.805	0.723
Susanna and the Elders	Ricci	18	Susanna	painting	standing	front	0.849	0.780
Adam and Eve	Santerre	18	Eve	painting	standing	front	0.763	0.700
Susanna and the Elders	Santerre	18	Susanna	painting	sitting	profile	0.808	0.726
Judgment of Paris	Troy	18	Venus	painting	standing	front	0.857	0.788
Judgment of Paris	Watteau	18	Venus	painting	standing	back	0.761	0.717

The three Graces	Antoine	18.5	Grace	sculpture	standing	front	0.779	0.728
Psyche Revived by Cupid's Kiss	Canova	18.5	Psyche	sculpture	lying	front	0.749	0.700
Venus	Coustou	18.5	Venus	sculpture	standing	front	0.816	0.763
Abandoned Psyche	David	18.5	Psyche	painting	sitting	profile	0.808	0.726
Cupid and Psyche	Gerard	18.5	Psyche	painting	sitting	profile	0.772	0.693
Adam and Eve	Marie	18.5	Eve	painting	sitting	profile	0.828	0.746
Cupid and Psyche	Michel	18.5	Psyche	painting	standing	front	0.764	0.701
Abandoned Psyche	Pajou	18.5	Psyche	sculpture	sitting	front	0.750	0.685
Susanna and the Elders	Vien	18.5	Susanna	painting	sitting	front	0.812	0.730
Susanna and the Elders	Beauvallet	19	Susanna	sculpture	standing	front	0.793	0.741
Adam and Eve	Blake	19	Eve	painting	standing	profile	0.833	0.766
The three Graces	Canova	19	Grace	sculpture	standing	back	0.784	0.751
Venus victrix	Canova	19	Venus	sculpture	lying	front	0.766	0.716
Susanna and the Elders	Chasseriau	19	Susanna	painting	standing	profile	0.855	0.787
Venus anadyomene	Chasseriau	19	Venus	painting	standing	profile	0.744	0.683
Venus in a shell	Christen	19	Venus	sculpture	sitting	profile	0.810	0.741
Adam and Eve	Dubufe	19	Eve	painting	sitting	front	0.771	0.692
Susanna and the Elders	Galland	19	Susanna	painting	sitting	profile	0.864	0.779
Ballerina Carlotta Chabert as Venus	Hayez	19	Venus	painting	standing	back	0.757	0.712
Susanna and the Elders	Hayez	19	Susanna	painting	sitting	back	0.766	0.706
Venus	Ingres	19	Venus	painting	standing	front	0.778	0.714
The Birth of Venus	Keller	19	Venus	sculpture	sitting	front	0.818	0.748
Venus	Mayer	19	Venus	painting	lying	profile	0.797	0.732
The Birth of Venus	Pradier	19	Venus	sculpture	lying	front	0.723	0.676
Psyché enlevée par des Zéphyrus	Prud Hon	19	Psyche	painting	lying	profile	0.818	0.752
Vénus au bain ou l'Innocence	Prud Hon	19	Venus	painting	sitting	front	0.823	0.740
The Birth of Venus	Rutxhiel	19	Venus	sculpture	standing	front	0.806	0.753
Venus lifting drapery	Simart	19	Venus	sculpture	standing	front	0.742	0.693
Susanna and the Elders	Tassaert	19	Susanna	painting	standing	profile	0.814	0.748
Cupid and Psyche	Thorvaldsen	19	Psyche	sculpture	standing	front	0.834	0.780
Venus with apple	Thorvaldsen	19	Venus	sculpture	standing	front	0.794	0.742
The three Graces	Thorvaldsen	19	Grace	sculpture	standing	profile	0.807	0.754
The power of Venus	Westall	19	Venus	painting	lying	front	0.789	0.725

The Birth of Venus	Amaury-Duval	19.5	Venus	painting	standing	front	0.758	0.696
La Vague et la Perle	Baudry	19.5	Venus	painting	lying	back	0.771	0.726
Venus anadyomene	Bocklin	19.5	Venus	painting	standing	front	0.799	0.734
The Birth of Venus	Bouguereau	19.5	Venus	painting	standing	front	0.750	0.688
Love and Psyche	Bouguereau	19.5	Psyche	painting	lying	front	0.778	0.714
Cupid and Psyche	Brocky	19.5	Psyche	painting	lying	front	0.777	0.714
The Birth of Venus	Cabanel	19.5	Venus	painting	lying	front	0.757	0.695
Susanna and the Elders	Cabet	19.5	Susanna	painting	sitting	profile	0.783	0.703
Adam and Eve	Collier	19.5	Eve	painting	standing	profile	0.716	0.657
Venus	Corot	19.5	Venus	painting	sitting	profile	0.812	0.730
Vénus poursuit Psyché de sa jalousie	Courbet	19.5	Venus	painting	lying	front	0.770	0.707
Susanna and the Elders	Dupuis	19.5	Susanna	painting	sitting	profile	0.837	0.753
The Birth of Venus	Gerome	19.5	Venus	painting	standing	front	0.720	0.660
The chaste Susanna	Henner	19.5	Susanna	painting	standing	profile	0.798	0.733
Adam and Eve	Jones	19.5	Eve	painting	standing	front	0.817	0.750
The three Graces	Jones	19.5	Grace	painting	standing	back	0.754	0.710
Venus	Klimt	19.5	Venus	painting	standing	front	0.740	0.679
Cupid and Psyche	Legros	19.5	Psyche	painting	lying	front	0.770	0.707
The Bath of Psyche	Leighton	19.5	Psyche	painting	standing	profile	0.772	0.709
Venus	Leighton	19.5	Psyche	painting	standing	front	0.764	0.702
Adam and Eve	Machell	19.5	Eve	painting	standing	profile	0.782	0.718
Adam and Eve	Moreau	19.5	Eve	painting	standing	front	0.824	0.757
Susanna and the Elders	Moreau	19.5	Susanna	painting	standing	profile	0.836	0.768
Judgment of Paris	Parrot	19.5	Venus	painting	standing	front	0.787	0.723
Venus	Picou	19.5	Venus	painting	lying	front	0.748	0.686
Susanna and the Elders	Ranson	19.5	Susanna	painting	standing	front	0.809	0.743
The Toilet of Venus	Rodin	19.5	Venus	sculpture	standing	front	0.747	0.698
The Birth of Venus	Selous	19.5	Venus	painting	lying	front	0.776	0.713
Venus	Stott	19.5	Venus	painting	standing	front	0.769	0.706
Cupid and Psyche	Swynnerton	19.5	Psyche	painting	standing	front	0.756	0.693
The three Graces	Valtat	19.5	Grace	painting	standing	front	0.757	0.695
Smiling Venus	Dali	20	Venus	painting	lying	profile	0.824	0.757
Venus with Cupids	Dali	20	Venus	painting	sitting	back	0.835	0.770

Loved Psyche	Denis	20	Psyche	painting	standing	front	0.765	0.703
The three Graces	Girieud	20	Grace	painting	standing	front	0.781	0.717
The Birth of Venus	Redon	20	Venus	painting	standing	front	0.780	0.717
Judgment of Paris	Renoir	20	Venus	sculpture	standing	profile	0.793	0.741
The Awakening of Psyche	Seignac	20	Psyche	painting	standing	front	0.715	0.655
Judgment of Paris	Simonet	20	Venus	painting	standing	front	0.767	0.704
Adam and Eve	Valadon	20	Eve	painting	standing	front	0.751	0.689
Susanna and the Elders	Vallotton	20	Susanna	painting	standing	front	0.830	0.763
Venus	van Loo	20	Venus	painting	standing	front	0.750	0.689
Venus	Watson	20	Venus	painting	standing	front	0.735	0.675
The three Graces	Watts	20	Grace	painting	standing	front	0.842	0.775
Venus	Bravo	20.5	Venus	painting	lying	profile	0.739	0.678
Sleeping Venus	Delvaux	20.5	Venus	painting	lying	profile	0.736	0.676
The three Graces	Moser	20.5	Grace	painting	standing	profile	0.792	0.727
Susanna and the Elders	Zaech	20.5	Susanna	painting	standing	front	0.781	0.718
Cupid and Psyche	Andersson	21	Psyche	painting	standing	back	0.720	0.678
Judgment of Paris	Cassez	21	Venus	painting	sitting	front	0.766	0.687
Susanna and the Elders	Chambon	21	Susanna	painting	lying	profile	0.735	0.675
Psyche's Doubt	Watwood	21	Psyche	painting	sitting	front	0.751	0.673

Encadré 7. Vénus et BMI



BMI des femmes symbolisant la beauté (Vénus, Aphrodite, Grâces) dans l'Art (peintures en violet et sculptures en jaune) en fonction du temps.

Par rapport au WHR, les tendances pour l'évolution du BMI considéré comme idéal au cours du temps sont moins claires, et la variance par période plus grande. Cependant, comme pour le WHR, le BMI semble rester constant durant l'Antiquité ($P = 0.35$), et diminuer à partir du XVe siècle ($\beta = -0.31$, $P = 0.016$).

III.3. Variations individuelles (Article 5)

Nous avons abordé l'effet des indices de fertilité immédiate sur l'attractivité (féminité faciale, WHR, BMI, F0), et avons démontré l'influence de la fertilité résiduelle sur l'attractivité, bien que les indices présents sur le visage nous sont encore inconnus. Qu'en est-il maintenant des traits du visage qui ne sont a priori pas reliés à la fertilité de l'individu (comme la couleur des yeux ou des cheveux) ? Ces traits « neutres » sont-ils sujets à la sélection sexuelle ? Et si oui, dans quel sens ? Dans cette étude, nous avons confronté deux hypothèses alternatives. La première va dans le sens d'une universalité de l'attractivité, puisqu'elle suggère que les hommes seraient majoritairement attirés par les femmes portant des caractères récessifs (Salter 1996; Laeng, Mathisen et al. 2007). Il s'agit de l'hypothèse de « certitude de paternité », selon laquelle les hommes pourraient utiliser les caractères phénotypiques présentant une héritabilité Mendélienne (ou quasi-Mendélienne) pour détecter leur paternité chez les descendants. Selon cette hypothèse, une partenaire portant des caractères récessifs faciliterait la transmission des caractères paternels (qu'ils soient récessifs ou dominants), et donc la détection de paternité. Or, la détection de paternité permet aux pères d'augmenter leur valeur sélective (en investissant uniquement dans leurs descendants légitimes), dans les espèces où l'investissement paternel est considérable, comme l'espèce humaine. La seconde hypothèse correspond à une variabilité individuelle des préférences, puisqu'il s'agit de l'hypothèse d'homogamie, c'est à dire une préférence pour la ressemblance à soi (Penton-Voak, Perrett et al. 1999) (voir partie I.3.iii).

Nous avons présenté à des juges masculins différents visages de femmes, réels et artificiellement créés par ordinateur, en leur demandant de choisir la plus attirante. Les traits du visages « neutres » et d'héritabilité de type Mendélienne étudiés étaient

notamment : la couleur des cheveux et des yeux (clairs ou foncés), l'épaisseur des lèvres et des sourcils (fins ou épais) et la fossette au menton (absence ou présence). Si les résultats de l'expérimentation avec les vrais visages n'a pas permis de conclure en faveur de l'une ou l'autre des hypothèses (le sens des préférences variaient en fonction du trait considéré), l'hypothèse d'homogamie est soutenue par l'expérimentation utilisant des visages artificiels (qui permettaient de contrôler expérimentalement tous les autres traits du visage, comme la féminité ou la symétrie) : Les hommes ont le plus souvent choisi comme étant le plus attirant le visage partageant le plus de traits en commun avec eux. Cette tendance se vérifiait pour chaque trait analysé indépendamment. Nous avons également cherché à savoir si ces préférences se retrouvaient dans les couples réels. Une analyse basée sur 155 couples Caucasiens a également révélé une tendance envers l'homogamie pour ces traits « neutres » du visage.

Cette étude montre qu'en plus des indices de fertilité (immédiate et résiduelle), les préférences masculines dépendent des caractéristiques physiques de l'individu exprimant ces préférences. De fait, le succès reproducteur d'un couple ne dépend pas uniquement de la fertilité de chacun des partenaires, mais également de leur compatibilité. Il peut exister plusieurs avantages évolutifs à l'homogamie. Lorsque la ressemblance est basée sur un grand nombre de traits, elle devient une mesure de la proximité génétique. Évidemment, une trop grande proximité génétique (entre proches apparentés) provoque une dépression de consanguinité (Bittles 2001; Jorde 2001; Das 2005; Postma, Martini et al. 2010). Mais il existe un mécanisme biologique (effet Westermarck) supprimant l'attirance sexuelle envers les proches apparentés et les personnes ayant vécu ensemble pendant l'enfance (Wolf 1970; Walter & Buyske 2003; Lieberman, Tooby et al. 2007). Ce mécanisme biologique est renforcé par des règles sociales interdisant les mariages incestueux (Bittles, Mason et al.

1991). Étant donné ces mécanismes permettant d'éviter la dépression de consanguinité, une préférence pour un certain degré d'homogamie peut être sélectionnée s'il existe aussi une dépression hybride. L'hybridation (« outbreeding ») peut diminuer la valeur sélective chez plusieurs espèces (Keller & Waller 2002 ; Edmands 2007). La dépression hybride peut être attribuée à la perturbation d'adaptations locales (culturelles ou génétiques), à la sous-dominance, ou à des interactions épistatiques. Il existe probablement un équilibre optimal entre consanguinité et outbreeding (Bateson 1978 ; Helgason, Snaebjörn et al. 2008). Il est donc possible que l'homogamie résulte d'une sélection pour éviter la dépression hybride, puisque la consanguinité est déjà restreinte grâce à d'autres mécanismes (biologiques et sociaux).

ARTICLE 5

Men's preference for women's facial features:
Testing homogamy and the paternity uncertainty
hypothesis

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Men's Preference for Women's Facial Features: Testing Homogamy and the Paternity Uncertainty Hypothesis

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Abstract

Male mate choice might be based on both absolute and relative strategies. Cues of female attractiveness are thus likely to reflect both fitness and reproductive potential, as well as compatibility with particular male phenotypes. In humans, absolute clues of fertility and indices of favorable developmental stability are generally associated with increased women's attractiveness. However, why men exhibit variable preferences remains less studied. Male mate choice might be influenced by uncertainty of paternity, a selective factor in species where the survival of the offspring depends on postnatal paternal care. For instance, in humans, a man might prefer a woman with recessive traits, thereby increasing the probability that his paternal traits will be visible in the child and ensuring paternity. Alternatively, attractiveness is hypothesized to be driven by self-resembling features (homogamy), which would reduce outbreeding depression. These hypotheses have been simultaneously evaluated for various facial traits using both real and artificial facial stimuli. The predicted preferences were then compared to realized mate choices using facial pictures from couples with at least 1 child. No evidence was found to support the paternity uncertainty hypothesis, as recessive features were not preferred by male raters. Conversely, preferences for self-resembling mates were found for several facial traits (hair and eye color, chin dimple, and thickness of lips and eyebrows). Moreover, realized homogamy for facial traits was also found in a sample of long-term mates. The advantages of homogamy in evolutionary terms are discussed.

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Introduction

Women's facial attractiveness reflects features that indicate high reproductive potential (for a review in humans, see [1]). For example, feminine characteristics are strong components of women's attractiveness and are linked to estrogen/androgen ratios—a reliable indicator of fertility potential [2]. However, some facial features, such as eye or hair color or dimples, do not exhibit any apparent association with individual fitness. These so-called “neutral features” have been proposed to be subject to sexual selection and are specifically linked to paternity confidence [3]. In this context, these traits are considered attractive because they increase the probability that paternal traits are expressed in the phenotype of the offspring, thereby facilitating the detection of paternity or non-paternity. Another hypothesis for the role of these facial features in mate choice is homogamy, where individuals demonstrate preferences for mates with similar genetic backgrounds [4,5,6]. In fact, mating with a partner of relatively proximal genetic background might be evolutionary advantageous by decreasing outbreeding depression. In this study, we aimed to simultaneously investigate the role of paternity confidence and homogamy in influencing the attractiveness of women's facial features.

In species where paternal care is required for the survival of the offspring, uncertain paternity might cause males to distinguish their own offspring from those conceived by their mate in extra-pair relationships [7]. In humans, some studies

have suggested that men are sensitive to cues of paternity when making decisions of paternal investment, such as fidelity and father-child facial similarities (in experiments [8], but see [9]; in real families [10,11,12,13,14]). If men assess their paternity through phenotype matching [15], then the phenotypic traits exhibiting Mendelian or quasi-Mendelian inheritance could be used to facilitate the detection of paternity or non-paternity. In this context, men displaying recessive features would demonstrate a preference for women exhibiting recessive versions of the same features, because their children will be phenotypically recessive for the trait, and a phenotypically dominant child could then signal a non-paternity. On the other hand, a phenotypically dominant man may conceive, with some probabilities, phenotypically dominant or recessive children, irrespective of the phenotype of his partner (the probabilities depend, among other, on allele frequencies in the population). Nevertheless, choosing a phenotypically recessive woman increases the probability that his dominant traits (rather than her recessive traits) will be expressed by their offspring, confirming transmission of paternal features (this probability is at least 0.5). As the number of dominant traits considered increases, the probability that at least one of them is transmitted also increases. Thus, the paternity uncertainty hypothesis predicts that both phenotypically dominant and recessive men prefer phenotypically recessive women, but this preference may be more important for recessive men.

An empirical evaluation of how preferences vary relative to one's own genetic determinism is available for eye color. Blue eye color is recessive to brown [16,17,18,19], and interestingly, a study has found that blue-eyed men tend to find blue-eyed women more attractive, whereas brown-eyed men were not found to exhibit a particular eye color preference [20] but see [21]. This result is consistent with eye color influencing attractiveness through a mechanism of enhanced non-paternity detection. This suggests that so-called neutral traits—in this case, eye color—might be subject to sexual selection. However, other unknown reasons (other than sexual selection) underlying eye color selection cannot be definitively excluded. Moreover, unless other polymorphic traits are also considered, the paternity uncertainty hypothesis cannot be validated. Indeed, the reliability of paternity confidence evaluation should increase with the number of traits evaluated. This is because the dominance effect blurs the relationship between phenotype and genotype, depending on the population frequency of heterozygotes. In particular, non-paternity detection using eye color is less reliable in a population where the majority of the population exhibits the same eye color, as there will be a high probability that the biological and the social fathers have the same eye color. Thus, when several dominant traits are simultaneously involved, the probability increases that at least one of them is transmitted and signals paternity.

Another hypothesis about the role of these so-called neutral facial features in mate choice is homogamy [4,5,6]. The extent to which there is selection for homogamy remains poorly understood and could result from an extension of a kin selection mechanism, as a lower genetic distance between parents translates into a higher parental-offspring relatedness (Genetic similarity theory, [22] or outbreeding avoidance [23]). Indeed, a majority of mates resemble each other for a high number of traits. Positive correlations have been demonstrated for socio-economic, psychological and physical variables [5,6,24,25]. Nevertheless, the observed formation of couples does not always reflect preferences. For example, if mate choice occurs within a given socioeconomic class [26,27,28], it will automatically generate homogamy for specific factors of each class. Competition for mates might also automatically generate homogamy for some features, such as attractiveness [29].

To simultaneously evaluate the paternity uncertainty (preferences for recessive states of features) and the homogamy (homogamy for facial traits independent of their dominance/recessive status) hypotheses, experiments were performed in which men were asked to rate the attractiveness of women's facial pictures. The dominance/recessive status of several facial traits was recorded for both women and raters. In Study 1, facial pictures from real women were used to investigate (i) whether raters prefer women with recessive facial features (i.e., paternity uncertainty hypothesis) and (ii) whether raters prefer women whose features are similar to their own, independently of the genetic determinism of these traits (i.e., homogamy hypothesis). In Study 2, the same test was also performed using artificial faces as stimuli to better control for the large number of dimensions involved in attractiveness. In all studies, these traits were first analyzed independently in the event of differing results, and then were simultaneously considered in order to provide an overall answer independent of specific traits. Finally, in Study 3, data derived from real couples were analyzed to evaluate whether the preferences previously identified are applicable to the formation of couples.

Materials and Methods

Ethics Statement

The protocol used to recruit participants and collect data was approved (#1226659) by the French National Committee of Information and Liberty (CNIL). For each participant, the general purpose of the study was explained (“a study on the determinants of facial attractiveness”) and a written voluntary agreement was requested for a statistical use of data (private information and photographs). Data were analyzed anonymously.

Study 1

Stimuli. Women between 18 and 25 years of age were recruited by social networks and in public places from Montpellier, Pau and Reims in France. For each woman, the following information was collected: place and date of birth, origin of parents and grandparents, socioprofessional category, monthly income (divided into nine classes from less than 760 € to more than 3618 €), and level of education. Three facial photographs (front, profile and three quarter views) were taken with the same digital still camera (Canon EOS 20D) at a distance of 1 m using the same general setting. Each individual was asked to express a neutral face and to remove any glasses or earrings. All photographs were electronically processed using Adobe Photoshop CS2 to normalize size, color balance, contrast and luminosity. The backgrounds were replaced by a uniform grey color. Each set of three facial views was assembled in a triptych (see figure 1).

Procedures. A Delphi-based computer program was generated to present randomly drawn pairs of triptychs to male raters (see figure 1). For each pair, the rater had to click on the picture depicting the woman he found the most attractive. The position of the picture on the screen (up or down) was randomly ascribed. A given rater had 20 distinct pairs of pictures to assess, corresponding to 40 different women. Three pairs, randomly chosen among those previously seen, were presented again at the end to estimate judgment reliability. Male volunteer raters were recruited in public places in Montpellier, France and were unaware of the purpose of the study when assessing pairs of women. For each rater, the following information was collected: date and place of birth, origins of parents and grandparents, monthly income, occupation, house ownership, taxability, education level and sexual orientation. After completing the evaluation of women's attractiveness, three facial photographs (front, profile and three quarter views) were taken for each rater using the same camera and conditions as above. The general purpose of the study was then explained (“a study on the determinants of facial attractiveness”) and a written agreement was requested to use the data (private information and the photographs).

Facial traits. A total of 16 variable facial traits with a quasi-Mendelian inheritance [17,18,19,30,31,32,33] were first considered. These features corresponded to various morphological features of the ear, eye, eyebrows, nose, chin, hair, mouth, skin and skull. These traits were classified among 400 triptychs as recessive or dominant by three independent evaluators (JB, MR and AA). Congruent scoring was statistically tested with a non-parametric Kappa test of concordance (K). Among congruent scores, seven features that were sufficiently frequent (>7%) in the studied population were selected for our study as follows: hair and eye color (dark or light, hair: $K = 0.48$, $P < 0.001$; eye: $K = 0.85$, $P < 0.001$), hair texture (curly or flat, $K = 0.37$, $P < 0.001$), chin dimple (presence or absence, $K = 0.50$, $P < 0.001$), thickness of lips and eyebrows (thick or thin, lips: $K = 0.55$, $P < 0.001$; eyebrows: $K = 0.57$, $P < 0.001$), and earlobe (attached or free, $K = 0.65$, $P < 0.001$). According to their known inheritance pattern, the states



Figure 1. A typical screen shot during the evaluation of the women's facial features by the raters in Study 1. Women aged 18–25 were recruited and three facial photographs (triptych) were taken. A computer program was used to randomly present drawn pairs of triptychs to male raters. For each pair, the rater had to click on the picture depicting the woman that he found the most attractive. The pictures and information were used with each woman's consent for publication.
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of these features were considered here as discrete variables, although this is an approximation due to the fact that 1) the exact genetic determinisms are not fully known, 2) there is a partial environmental influence [34], and 3) some traits (e.g. lips thickness) display a unimodal distribution when quantitatively measured (unpublished results). These seven traits were typed for all female participants and male raters.

Morphological measurements. Twenty-one points of interest were positioned on the front face photograph of each female participant [35,36] (see figure S1). Differences between 8 corresponding distances on each side of the face were calculated for each woman. Each difference was weighted by the mean of the two corresponding distances. A Principal Component Analysis (PCA) was performed on the resulting four variables to obtain a new synthetic variable corresponding to an asymmetry axis. The coordinate of each woman along this axis represents her individual asymmetry synthetic value. To assess femininity, 9 distances were computed from the same twenty-one points for all women subjects. Similar measurements were performed on a random sample of sixty males (derived from the raters). A linear discriminant analysis (LDA) according to sex was performed on the male and female measurements, providing a synthetic variable corresponding to a masculinity/femininity axis. The coordinate of each woman along this axis represents her individual femininity value (see figure S2). The contrast between lip and skin color was also measured. Pictures were converted to black and white, and grey values were measured for four points on the lips and four points on skin around

the mouth. The difference between the means of the grey values of the lips and skin was used as a contrast value. All morphological measurements were performed using Image J software, version 1.43.

Statistical analysis. Logistical regression was used to analyze raters' preferences. The response variable corresponded to being chosen or not for each woman during the presentation of each pair (binary variable). Women and raters were considered random samples from a larger population of interest and were thus random-effect variables. Therefore, generalized linear mixed models with binomial error structure were used. A recessivity index was created that varied from 0 (no recessive trait displayed by the woman) to 7 (all traits considered displayed the recessive variant by the woman). For each choice made by a rater, the difference between the recessivity indices of the focal and the non-focal woman was calculated. The value of this difference (variable "recessivity") was integrated into the models. Then, a homogamy index was created. For each woman, the number of traits for which a common state (recessive or dominant) was shared with the rater was scored. The difference between the two women subjects for this score was entered into the model (variable "homogamy"). This score varied from 7 (the focal woman exhibited all traits in common with the rater whereas the non-focal exhibited none) to -7 . To control for potential confounding effects, other variables were included in the models. These variables included the following factors: the rater's age, and socioeconomic status (a PCA combination of the variables "monthly income", "occupa-



Figure 2. An example of a quartet used in Study 2. A Delphi-based computer program was used to present the virtual women's faces. For a given rater, four faces of the same virtual woman were selected, depending on the rater's own traits (initially recorded in the computer program by the observer; see table 1). These four faces corresponded to the four cases of preferences: homogamy (the face displayed similar character states as the rater), heterogamy (the face displayed opposite character states), recessivity (the face displayed recessive character states) and dominant (the face displayed dominant character states). The rater was instructed to click on the woman that he would prefer to build a family with. Images are from virtual subjects.

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tion", "house ownership", "taxability" and "education level"), as well as variables affecting women's attractiveness, such as fluctuating asymmetry, degree of femininity, lip contrast and age. For asymmetry and femininity, non-linear adjustments were explored. Because in some photographs the women subjects displayed a perceptible smile, a qualitative variable describing this aspect (absent, slightly perceptible, perceptible) was also introduced as a potential confounding effect on attractiveness. Indices of homogamy and recessivity were also calculated for each trait independently. These 7 binary variables were used in a model where only significant confounding variables of the previous model were added (the age of the raters and of the women subjects, smile, asymmetry and femininity). The data were analyzed by multi-model inference [37,38]. The fits of all possible models were compared using AIC, allowing their Akaike weights to be calculated (R package MuMin). Model averaging was performed on all models, weighting the contribution of each model according to its Akaike weight [39]. The relative importance of each variable (the sum of the Akaike weights of the models in which the variable appears) and the averages of estimates (weighted by Akaike weights) were calculated. All statistical analyses were performed using R 2.14.0 software (R Core Development Team, 2005).

Study 2

Stimuli. A total of 15 distinct virtual faces were created. FaceGen software permits to create artificial 3D faces varying for general face shape, lips and eyebrows (width, thickness, color), and expression (smile). Different hair styles and color (dark or light) were added with TAAZ software. Using Photoshop, eye color (dark or light) and chin dimple were modified. Variations of the five traits under study (see below) were within the normal range of variation displayed by stimuli of Study 1 (details not shown).

Procedure. For each rater, the same information as in Study 1 was collected. During a preliminary questionnaire, an observer recorded the state of the five traits (hair and eye color, chin dimple, and thickness of lips and eyebrow) from the rater's face. A Delphi-based program was used to present the virtual women's faces. For a given rater, four faces (a 'quartet'; see figure 2) were selected, depending on the rater's own traits that were initially recorded in the computer program by the observer (see table 1). Within a quartet, only 5 features of interest vary: hair and eye color (dark/light), chin dimple (present/absent), and thickness of lips and eyebrows (thick/thin). Other characteristics (shape of the face,

nose, expression, hair style), vary between quartets. The four faces corresponded to the four cases of preferences: homogamy (the face displayed similar character states as the rater), heterogamy (the face displayed opposite character states), recessivity (the face displayed recessive character states) and dominant (the face displayed dominant character states). These four faces were presented in a row, in a random order. The rater was instructed to click on the woman subject that he would prefer to build a family with. Among the five features studied, three are generally considered to be independent of women's attractiveness (hair and eye color and chin dimple) and two are known to be femininity or attractiveness cues ("lips" and "eyebrows"; thick eyebrows are considered as more masculine and thick lips as more attractive [1]). To control for the effect of lips and eyebrows in influencing perceived attractiveness, raters were randomly separated into two groups. The first group was presented faces varying for eyes, hair, chin dimple and eyebrows (the state of the lips was in this case randomized between the quartets but constant within each quartet). The second group was presented faces varying for eyes, hair, chin dimple and lips. Each rater evaluated fifteen quartets, in a random order. To estimate judgment reliability, two quartets randomly chosen among those previously seen were presented at the end. Caucasian male volunteers were recruited in public places in Montpellier, France and were unaware of the

Table 1. Example of facial features for the four women appearing in a quartet in Study 2.

Women (hypothesis)	Facial features				
	Eyes	Chin dimple	Hair	Eyebrows	Lips
Woman 1 (homogamous)	light	no	dark	thick	thin
Woman 2 (heterogamous)	dark	yes	light	thin	thick
Woman 3 (recessivity)	light	no	light	thin	thin
Woman 4 (dominance)	dark	yes	dark	thick	thick

The rater's traits were recorded in the computer program. Then, the four faces of the same virtual woman were presented, depending on the rater's own traits (see figure 2). An example for a rater with light eyes, no chin dimple, dark hair, thick eyebrows and thin lips.

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purpose of the study when assessing quartets of women. A written agreement was obtained for usage of their private information.

Statistical analysis. The response variable was the preferred face of each rater. This variable included four modalities (homogamy, heterogamy, recessivity and dominant). Artificial faces and raters were considered random samples from a larger population of interest, and thus, both groups were considered to be random-effect variables. However, no multinomial model with random-effects was available with R 2.14.0 software. To overcome this limitation, two approaches were used. First, one response by each rater was randomly sampled, and a multinomial model was applied. The process was repeated 1,000 times, generating a distribution of P -values. Second, the data were analyzed by multimodel inference as in Study 1. One of the four positions was arbitrarily chosen (the first on the left), and the variable responses reflected the choice of each rater on that position (yes if chosen, no if otherwise). As in Study 1, confounding variables were added to test the effects of the raters' characteristics (age and socioeconomic status) on their choices. Next, the homogamy and recessive indexes were calculated as in Study 1. We created overall indices for all of the traits together, plus indices for each characteristic independently. The fits of all possible binomial generalized linear mixed models were compared, and the relative importance and the weighted average of the estimates for each variable were calculated as in Study 1.

Study 3

Procedure. Couples were recruited through our social acquaintances and in public places of Paris, Hyères, Grenoble and Montpellier in France. They are all Caucasian and have at least one child (a factor that we used to ensure that the couples were in long-term relationships at the time of the study). For each couple, the man and the woman were classified by three independent evaluators (AA, JB and MR). The five characteristics studied were the same as in Study 2: hair and eye color, chin dimple, and thickness of the lips and eyebrows.

Statistical analysis. For each trait, the association of the phenotypes of mates was tested using a one-sided Fisher's exact test on a 2×2 contingency table, with homogamy as the alternative hypothesis. To generate a global test for the five traits, a joint distribution of the five tables was generated by 1000 resampling with the same marginal counts for each table. The product of the odd-ratio of each of the five-sample tables was used as a statistic. The proportion of these statistics that was higher than or equal to the observed value was used as an estimation of the P -value.

Results

Study 1

We quantified the attractiveness of young women using their facial pictures. We investigated whether men are more likely to prefer women with more recessive traits or with traits similar to their own.

Final sample. A total of 59 young women were sampled (age range: 18–25, mean = 22.4). Three hundred and sixty-one male raters assessed the relative attractiveness of these women. Assessments from unreliable raters (i.e., with more than one incorrect answer during the test of judgment reliability) were removed. A total of 345 raters were retained in the final sample, all Caucasian and heterosexual, with a mean age of 27.1 (age range: 18–61).

Importance of recessivity and homogamy. The relative importance (I) of each variable demonstrated with high probability that the recessivity index is in the best approximating model, with

a negative effect (averaged parameter estimate $\beta = -0.10$; $I > 0.99$) on the probability for a woman to be chosen. A majority of men preferred women with more dominant features. There was a positive effect ($\beta = 0.04$; $I = 0.80$) of the homogamy variable. To more precisely understand male preferences, the same indices were tested trait-by-trait in a secondary model. Although the dominant state of lips, eyes and earlobes were significantly preferred ($I > 0.99$), there was a significant preference ($I > 0.99$) for the recessive state of the eyebrows and chin dimple, and the thickness of lips was significantly preferred when homogamous ($I = 0.65$).

Importance of other women's characteristics. Several variables demonstrated a significant probability to be in the best approximating model: Young ($\beta = -0.28$; $I = 0.91$) and more frequently smiling ($I > 0.99$) women were more likely to be chosen by raters. The "asymmetry" variable was adjusted for using the function: $\times + \exp(x)$. More symmetric women were more often chosen ($\beta = -0.04$; $I > 0.99$). The factor $\exp(x)$ indicates that attractiveness decreases faster than linearly with asymmetry. To determine the effects of femininity, the association between the degree of smiling and squared femininity was analyzed. Attractiveness increased with femininity, especially if the woman was smiling. Lip contrast did not exhibit a significant probability to be in the best approximating model ($I = 0.49$).

Effects of raters' characteristics. The raters' ages ($I = 0.85$) and socioeconomic levels ($I = 0.61$) exhibited a significant probability to be in the best approximating model.

Study 2

To differentiate the effects of recessivity and homogamy from other predictors of attractiveness, we conducted an experiment similar to that performed in Study 1 using artificial faces.

Final Sample. One hundred and sixty-nine male raters expressed their preference. Assessments from unreliable raters (i.e., with more than one incorrect answer during the test of judgment reliability) were removed. Individuals with all the 5 features studied in the recessive (or dominant) state were also removed. A total of 99 raters were retained in the final sample, all Caucasian and heterosexual, with a mean age of 37.3 (age range: 19–84). A multinomial test was used on a sample of 1 response from each rater (randomly sampled for each rater among the fifteen women tested). This process was repeated 1,000 times, generating a distribution of P -values.

Homogamy and recessivity: general indices. The most frequent choice (37%, $P = 0.036$, see figure 3) tended to be the women presenting similar facial features as the rater. Thus, women presenting similar phenotypes as the raters themselves were predominantly preferred (homogamy). The multimodel inference on the binomial generalized linear mixed model showed that the homogamy index exhibited a significant probability to be in the best approximating model ($\beta = 0.40$; $I > 0.99$) but not the recessivity index ($\beta = 0.00$; $I = 0.27$). The raters' age exhibited a significant probability to be in the best approximating model ($I > 0.59$). The raters' choices were not influenced by SES ($I = 0.29$).

Homogamy and recessivity: analysis by facial trait. The same tendency toward homogamy was significant for all of the facial features analyzed individually: eye color ($\beta = 1.12$; $I > 0.99$), hair color ($\beta = 0.73$; $I > 0.99$), chin dimple ($\beta = 0.98$; $I > 0.99$), and lip ($\beta = 0.55$; $I > 0.99$) and eyebrow thickness ($\beta = 1.29$; $I > 0.99$). We also found a considerable effect of the traits' absolute state. Raters exhibited a preference for the dominant state of two features: brown eyes ($\beta = -0.21$; $I = 0.69$) and dark hair ($\beta = -0.47$; $I = 0.99$). The recessive state was preferred for the three other features: chin dimple absence ($\beta = 0.30$; $I = 0.82$), thin

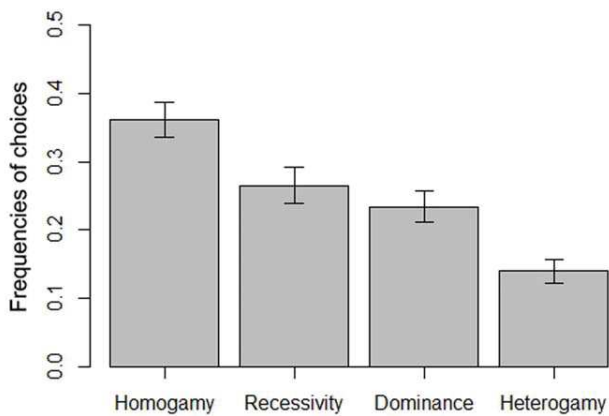


Figure 3. The raters' choices according to the artificial faces hypotheses in Study 2 (See figure 2). The raters predominantly preferred faces similar to their own.
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lips ($\beta = 0.26$; $I = 0.66$) and eyebrows ($\beta = 1.29$; $I > 0.99$). However, these effects might be the consequence of homogamy that is linked to unbalanced traits within the raters' sample. For example, more than 80% of raters had brown hair, and they mainly preferred women with brown hair. This hypothesis was confirmed by separating raters according to their own traits (two groups for each characteristic). Preference for homogamy according to specific facial features appeared to best explain these results. Global preference toward homogamy remain unchanged even when quartet where some faces differed by only one trait were removed (corresponding to raters with almost all features in dominant or recessive state).

Predictions of paternity uncertainty hypothesis and the homogamy hypothesis. Consistent with the homogamy hypothesis, phenotypically dominant men prefer phenotypically dominant women, and phenotypically recessive men prefer phenotypically recessive women (see table 2). Contrarily to the paternity uncertainty hypothesis, there is no support for a lower assortation for dominant traits compared to recessive traits. The only exception is for the eyebrows (see table 2), probably due to the fact that thin eyebrows are considered as more feminine, and so more attractive [1]. Thus phenotypically dominant men could be attracted by women with thin eyebrows too, limiting the homogamy effect for this specific feature.

Study 3

Here, we investigated whether the preferences observed during experiments are actually applied in real mate choice. We therefore determined whether the trends of facial homogamy identified in Studies 1 and 2 were significantly conserved in a sample of real couples. The analysis was based on 155 Caucasian couples. First, the partners were analyzed trait-by-trait using Fisher's exact tests. There were positive but non-significant associations (when corrected for multiple testing: confidence threshold = 0.05/5 tests = 0.01) for lip thickness ($OR = 2.44$, $P = 0.023$), eye color ($OR = 1.38$, $P = 0.22$), hair color ($OR = 1.41$, $P = 0.35$), and chin dimple ($OR = 3.61$, $P = 0.45$). There was also a negative and a non-significant association for eyebrow thickness ($OR = 0.69$, $P = 0.89$). Next, the combined 5 traits were analyzed together. A significant trend toward overall homogamy was revealed ($P = 0.018$). These results suggested that couple formation is driven by a global similarity rather than a homogamy for particular traits. It is also

Table 2. Testing the homogamy and the paternity uncertainty hypotheses, according to raters and women's phenotypes.

Traits	Homogamy		Paternity uncertainty
	DD>RD	and RR>DR	RR>DD
Eyes	<10-5	<10-5	0.73
Hair	<10-5	0.14	0.992
Chin	0.00255	<10-5	0.17
Lips	0.07	0.00003	0.28
Eyebrows	0.43	<10-5	0.00015
All	<10-5	<10-5	0.39

Predictions are coded as follows: the first letter indicates the phenotype of women preferred, and the second the rater's phenotype. Thus "DD>RD" corresponds to the hypothesis "the preference of phenotypically dominant men towards phenotypically dominant women is stronger than the preference of phenotypically recessive men towards phenotypically dominant women". P-value for each trait and overall are presented. Bold P-values highlight significant ($P < 0.05$) results.

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possible that men prefer women with all traits corresponding to their own but that the realization of these preferences during mate choice is incomplete and cannot be achieved for all facial features.

Discussion

Although there is abundant evidence showing that cues indicating reproductive potential are considered attractive in women, few empirical studies have investigated the role of other selective pressures on men's mate choice, particularly considering that choice is not absolute but is also relative to the men's phenotype. This study investigates whether facial traits are more attractive if they are (i) recessive phenotypes, increasing the probability that subsequent offspring will exhibit a phenotype that facilitates paternal recognition (Salter's paternity uncertainty hypothesis [3]), and (ii) phenotypically similar to the facial traits of the rater (e.g., homogamy), which might indicate optimum genetic compatibility between mates. These hypotheses were tested on seven facial traits using both actual and virtual facial stimuli. The predicted preferences were then compared to realized mate choices using the facial pictures from couples with at least 1 child. Our data suggest that men prefer facial traits similar to their own, in both preference experiments and actual mate choice. Our results, however, do not support the hypothesis that men prefer women with traits that facilitate the detection of paternity/non-paternity in their offspring.

The raters of our study did not exhibit particular preferences for women's recessive facial traits, contrary to the prediction of the paternity uncertainty hypothesis. Thus, women's facial attractiveness does not appear to comprise a signature of paternity confidence, at least not as proposed by Salter [3]. An empirical knowledge of inheritance rules is required to discern whether mate preference can evolve according to the Salter hypothesis. Despite evidence for the common knowledge of inheritance [40,41], several uncertainties prevent the application of this general knowledge to specific features. First, the low population frequency of some heritable features prevents the development of an intuitive comprehension of their mode of inheritance (e.g., freckles, red hair, white forelock). Second, non-heritable features, such as various types of spots, pimples, infantile haemangioma, angioma, result in a confounding background noise for any attempt to

decipher how other specific traits are inherited. Third, the exact genetic determinism is often more complex than the simple Mendelian inheritance considered here, and a non-negligible environmental influence contributes to obscure the inheritance pattern [34]. Moreover, the instability of some facial traits in newborns compromises the reliability of those traits for the inference of paternity. For example, eye color, for which the recessive state (blue) is often first expressed in young babies (at least for Caucasian individuals), is replaced by a brown (or green or grey) color for those possessing the corresponding allele later in life [42]. Such is also the case for hair color, with a longer expression of the recessive state (blond). This could correspond to an anonymization of the baby, as the phenotypes of babies with those features tend to be similar—independently of their parents' genotype. Indeed, children may benefit from anonymization in some circumstances (*i.e.*, in the case of non-paternity) [43]. It is known that such anonymization is parent-specific, as newborn babies tend to resemble their mothers [12,44,45,46], but see [47,48]. Why some features are partially anonymized whereas others are not remains an open question. There is the intriguing possibility that the process of anonymization could be restricted to traits that exhibit Mendelian inheritance because of the constraints associated with traits coded by many genes. This, in turn, decreases the extent of selection that assesses paternity confidence based on traits that exhibit Mendelian inheritance.

This study provides evidence for the homogamy for certain facial features. The male raters in this study preferred women's faces that exhibited the same states as themselves for five out of the seven traits investigated (eye color, hair color, chin dimple, thickness of lips and eyebrows). This finding was revealed when artificial faces were used (Study 2) and only partially revealed (thickness of lips) when faces from real women were used (Study 1). Although many dimensions comprise facial attractiveness, only two have been controlled for in experiment 1 (overall femininity and symmetry). Men have been previously demonstrated to prefer the most attractive female faces rather than self-resembling ones, although when attractiveness was controlled for, the self-resembling faces were preferred [49]. This probably explains the discrepancy between the results of Study 1 (where two attractiveness components were statistically controlled for) and Study 2 (where all attractiveness components were experimentally controlled for). To avoid false statistical associations among traits that might result from the numerous dimensions involved in facial attractiveness, a very large sample size is required. In a limited sample, an apparent preference for a trait can arise indirectly: it could reflect a preference for another trait associated by chance within the sample. Conversely, Study 2 used a protocol that adjusts artificial faces of the experiment to each rater's face, while controlling for non-relevant variables. A limitation of Study 1 is that the question asked to the raters ("which of the 2 women is more attractive?"), was not explicitly proposed in a context of long or short-term relationship, which can influence preferences [50].

Why would self-resembling mates be preferred? When resemblance is based on a large number of genetically heritable traits, it becomes a measure of genetic proximity. Due to the known inbreeding depression in most human societies [51,52,53,54], mate preference based on high resemblance (*i.e.*, toward close kin) should be avoided. Indeed, self-resemblance decreases attractiveness in a short-term sexual context [55]. This avoidance is in fact enforced by a biological mechanism (Westermarck effect) that suppresses sexual attraction toward co-residents during childhood—generally siblings or close members of kin [56,57,58,59]. This biological mechanism is further reinforced by social rules forbidding incestuous marriages, where the definition

of incest is based on family linkage (with a large cultural variation) [60]. Considering these mechanisms enforcing avoidance of inbreeding depression, some degree of homogamous mate preference should develop only if there is also an extent of outbreeding depression. Outbreeding can induce a loss of fitness in several species [61,62]. Outbreeding depression can be attributed to the disruption of local adaptation (cultural or genetic), underdominance, or epistatic interactions. Ideally, there should be an optimal balance between inbreeding and outbreeding [63]. Interestingly, in Iceland, the greatest reproductive success is for couples related at the level of third and fourth cousins, with a decrease in fertility for closer or more distantly related couples [23]. It is thus possible that homogamy results from a selection for avoiding outbreeding depression, given that inbreeding is already prevented by other mechanisms (biological and social).

The homogamy hypothesis is possibly confounded by the familial imprinting effect *e.g.* preference for the face of the opposite-sex parent [24,64,65]. However, because children resemble their parents, it's difficult to distinguish between effects of familial imprinting and homogamy (self-referential phenotype matching). Clearly, there is also the possibility that preference for the face of the opposite-sex parent correspond to a preference for homogamous mating. Nevertheless, it seems that these two mechanisms exist, and have context-specific effects [66].

Mate preference does not readily translate into actual mate choice, due to mate competition and social subdivisions. It is even possible that traits considered to significantly influence attractiveness do not exert effective influence on actual pairing [29], suggesting that preferences might not always be readily deduced from observed pairing. The observed homogamy in real couples for the five facial features examined in our study suggests that preference for homogamous mating has operated. There are, however, several potentially confounding phenomena that might account for apparently homogamous mating. For instance, if there is competition in both sexes for long-term mates, a similarity between romantic partners would result as a side effect [67]. Attractive individuals might pick their own preferred (and attractive) mate from the pool of those available, leaving less attractive individuals to pair with those that remain unpaired. Thus, homogamy might result from such a process, despite the fact that all individuals prefer the same category (attractiveness) for mates. However, as raters in this study did not prefer the same features (their preferences depended on their own traits), this process is unlikely to apply here. Similarly, resemblance could result from long-term environment sharing, rather than from preferences at the time of couple formation [5,6,25]. However, the traits considered here mainly have a genetic basis and are thus not particularly prone to such effects. Homogamy might also result from social proximity. Indeed, people are more likely to meet their mate within their own social class; thus, there is a high probability that they will share traits that are specific to this class. A prerequisite for this hypothesis is that the features involved are differently distributed across social classes. To our knowledge, the distribution of facial features across social classes has not been studied.

Homogamy in the context of the facial features examined in our study has already been reported for hair color (0.28) and eye color (0.21) [20,68]. Concerning preferences, Laeng et al. [20] found that, consistent with our study, blue-eyed men tended to rate blue-eyed women as more attractive than brown-eyed ones. However, they also found that brown-eyed men exhibited no preference for blue- or brown-eyed women. In contrast, we observed that brown-eyed men found brown eyes women more attractive. The reasons for this discrepancy are unclear and might originate from

differences in experimental design (e.g., manipulated photographs of real faces versus manipulated artificial faces; attractiveness scale versus choice among alternatives), true cultural differences (e.g., Norway versus southern France) or random effects (e.g., the number of raters was about 4-fold larger in the present study). Future studies are warranted to clarify this point.

Women's facial attractiveness is complex and includes many components. Paternity signaling is not a significant component of attractiveness, at least within the experimental context of this study. Mate similarity, although certainly not a predominant component compared to fertility cues, is likely a component that should be thoroughly controlled for in future studies of homogamous preference. Further studies are necessary to verify whether the preference for homogamous traits is favored as a way to avoid outbreeding and its associated fitness costs. Although these costs have been delineated in many other species, they remain to be investigated in humans. Finally, the underlying mechanisms of outbreeding depression need to be better understood.

Supporting Information

Figure S1 Points for measurement of asymmetry and femininity. For asymmetry, eight distances on each side of the face were considered: (2-3) vs (4-5), (15-17) vs (18-20), (16-8) vs (19-

9) and (3-21) vs (4-21). For femininity/masculinity, nine distances were computed: (2-5), (3-4), (6-7), (8-9), (11-12), (10-13), (2-14), (1-14) and (11-14). (TIF)

Figure S2 Linear discriminant analysis (LDA) according to sex. It provides a synthetic variable corresponding to a masculinity/femininity axis. The coordinate of each woman along this axis represents her individual femininity value. (TIF)

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Author Contributions

Conceived and designed the experiments: J. Bovet J. Barthes MR AA. Performed the experiments: J. Bovet J. Barthes VD MR AA. Analyzed the data: J. Bovet J. Barthes MR. Wrote the paper: J. Bovet MR AA.

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I. Discussion

I.1. Les différentes facettes de l'attractivité

i. Des critères variés

Les résultats de cette thèse confirment que les hommes utilisent des indices présents dans l'apparence physique des femmes pour choisir une partenaire. Ces indices peuvent être liés à la fertilité immédiate (capacité actuelle d'une femme à engendrer un descendant), mais aussi à la fertilité résiduelle (nombres de descendants potentiels qu'une femme pourra avoir dans le futur). Les éléments de l'attractivité physique utilisés peuvent se situer sur une échelle absolue, indépendante de l'observateur (préférence pour un faible WHR par exemple), ou sur une échelle relative, dépendante des caractéristiques de l'observateur (homogamie pour les traits du visage par exemple). Dans ce dernier cas, il ne s'agit plus seulement de la fertilité de la femme, mais également de la fertilité du couple, liée à la compatibilité entre les deux partenaires.

Durant cette thèse, nous nous sommes concentrés sur l'attractivité physique, et plus particulièrement sur les zones du visage et le WHR. Cependant, pour choisir une partenaire, les hommes utilisent évidemment de nombreux autres traits visuels, mais aussi olfactifs ou auditifs (l'aspect tactile de l'attractivité est peu étudié mais est probablement aussi en jeu). En outre, même si la part de l'attractivité « statique » (visible sur une photo) est considérable dans le choix d'une partenaire, il existe aussi des indices dans les mouvements, la façon de parler, ou plus généralement de se comporter, pouvant être liés à la condition physique, la psychologie, ou encore au milieu social.

ii. Des critères hiérarchisés

Pour juger la valeur reproductive de chaque partenaire potentielle, un homme est donc confronté à un grand nombre d'indices plus ou moins indépendants les uns des autres. Les individus doivent alors trier ces différentes informations, et il existe vraisemblablement une hiérarchie entre les différents critères d'attractivité. En effet, les critères d'attractivité *absolus* (symétrie, dimorphisme sexuel) ont plus d'importance sur l'attractivité des visages que les critères *relatifs* comme l'homogamie (Penton-Voak, Perrett et al. 1999; Saxton, Little et al. 2009; Kocsor, Rezneki et al. 2011). Ce principe de hiérarchisation a également été trouvé chez des souris : les femelles préfèrent les mâles dominants, qu'elles identifient grâce à des indices olfactifs dans l'urine, liés aux androgènes (qualité génétique sur une échelle absolue), et basent leur choix sur une échelle relative, la dissimilarité du CMH, seulement s'il y a peu de variation de la qualité génétique entre les mâles (Roberts & Gosling 2003). Bien que la hiérarchie des différents critères d'attractivité n'ait pas directement été abordée durant cette thèse, les résultats de l'article 5 indiquent que, si les hommes expriment bien une préférence pour l'homogamie des traits *neutres* du visage, elle semble secondaire par rapport aux critères *absolus* de fertilité.

Quoiqu'il en soit, collecter, intégrer et hiérarchiser toutes ces informations implique une mobilisation importante des ressources cognitives. Nous avons identifié dans l'article 1 l'utilisation par les hommes de leur vision périphérique lors du jugement de l'attractivité d'un corps féminin. Limiter l'information perçue à l'information nécessaire (seule la forme globale du corps est importante, les détails pouvant se trouver au niveau du contour de la silhouette sont superflus) peut être un moyen de simplifier le processus. Nous retrouvons l'hypothèse de la forme du corps comme étant une sorte de « premier filtre » (Singh 1993) :

cruciale dans le jugement de l'attractivité, mais ne nécessitant pourtant que peu d'attention tant son évaluation est rapide. Plus encore, la vision périphérique pourrait être le meilleur moyen d'obtenir une vision d'ensemble, le regard direct ne permettant pas de détecter une forme globale. Cette étude ne nous permet par contre pas de déterminer si cette forme globale du corps correspond plutôt au BMI ou au WHR. Il existe actuellement un débat quant à la part relative du BMI et du WHR dans l'attractivité féminine. Ces deux indices sont liés à la santé et à la fertilité, et sont intrinsèquement corrélés l'un à l'autre, de telle sorte qu'il est très difficile de séparer leur rôle dans l'attractivité.

iii. Des préférences variables

Les préférences pour les traits situés sur une échelle *relative* sont variables entre les individus, car la valeur la plus intéressante de ce trait (du point de vue du succès reproducteur) dépend du phénotype de l'individu qui exprime la préférence. C'est ce qui se passe pour les traits « neutres » du visage, pour lesquels nous avons observé une préférence pour l'homogamie. Par contre, pour les traits situés sur une échelle *absolue*, les préférences devraient se porter invariablement sur la valeur optimale de ce trait (par exemple la valeur du WHR correspondant à une fertilité maximale). Or, durant cette thèse, nous avons démontré l'existence de variations, géographiques et temporelles, des préférences pour plusieurs de ces traits à l'échelle *absolue*.

Une variation des préférences est-elle la signature d'une adaptation, ou celle d'une norme culturelle arbitraire ? Pour certains, l'universalité des préférences est utile, sinon nécessaire, pour prouver leur origine évolutive : « *A good working proof of a psychological adaptation is its universal nature* » (Tovee, Maisey et al. 1999). Nous soutiendrons ici que l'universalité d'une préférence n'est pas une preuve qu'elle ait été sélectionnée, pas plus que

sa variation n'est la marque d'une origine culturelle. Prenons comme exemple la couleur de la peau. L'aspect plus ou moins sombre de la peau humaine est une adaptation à la quantité du rayonnement solaire, et varie entre les populations en fonction de leur situation géographique (Jablonski & Chaplin 2000). Il est attendu que les préférences pour la couleur de la peau varient de la même façon, car choisir une partenaire à la peau trop claire dans une région où le rayonnement solaire est fort aura des conséquences négatives sur le succès reproducteur. Dans ce cas précis, une variation géographique des préférences sera donc le résultat d'une adaptation, et à l'inverse, une préférence universelle pour une couleur de peau en particulier (blanche par exemple) pourrait très bien être la marque d'une standardisation culturelle (due à la surreprésentation des individus à la peau claire dans les médias par exemple).

I.2. Une histoire de compromis

Une variation des préférences (pour des traits situés sur une échelle *absolue*) cache souvent l'existence d'un compromis. Dans l'exemple de la couleur de la peau cité ci-dessus, il existe un compromis entre la captation d'une quantité suffisante d'UV nécessaire à la production de vitamine D, et la protection des effets néfastes des UV (brûlures, cancer de la peau, photolyse du folate) (Jablonski & Chaplin 2000). Du fait de ce compromis, la couleur optimale de la peau va varier géographiquement en fonction du rayonnement solaire.

i. L'exemple de la masculinité

Il existe un autre exemple bien documenté d'un compromis engendrant une variation des préférences en fonction des conditions environnementales. Il concerne la préférence des femmes pour la masculinité. Dans la première partie de cette thèse, nous avons mentionné

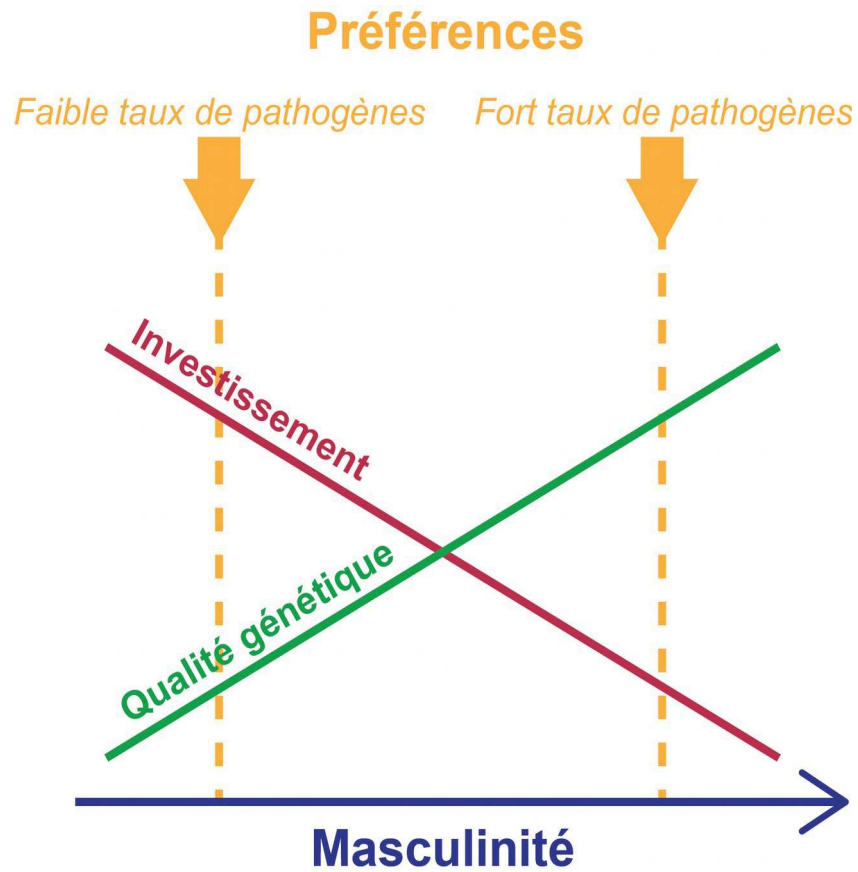


Figure 1. Illustration du compromis, chez les hommes, entre qualité génétique et investissement. Les préférences des femmes pour la masculinité vont varier en fonction de conditions environnementales (par exemple le taux de pathogènes), afin de maximiser l'une ou l'autre de ces qualités.

l'existence du compromis existant, chez les hommes, entre la qualité génétique (signalée par une masculinité élevée), et l'investissement (envers la partenaire ou les descendants) (DeBruine, Jones et al. 2010). Dans un environnement hostile, où la mortalité extrinsèque est élevée, les femmes peuvent maximiser leur valeur sélective en se concentrant sur l'acquisition d'une bonne qualité génétique pour leurs descendants, afin qu'ils puissent survivre dans cet environnement. A l'inverse, dans un environnement avec un faible taux de mortalité, la probabilité de survie des enfants et de leur reproduction éventuelle est plus élevée, et choisir un partenaire capable d'investir peut permettre de canaliser les ressources pour les descendants. La valeur optimale de masculinité va donc varier en fonction des conditions environnementales, et il est attendu que les préférences féminines varient en conséquence. Plusieurs études inter-culturelles montrent que c'est effectivement le cas : la préférence des femmes pour la masculinité des visages est positivement corrélée au taux de pathogènes, et négativement corrélée aux conditions de santé d'une population (Penton-Voak, Jacobson et al. 2004; DeBruine, Jones et al. 2010; DeBruine, Jones et al. 2011). De plus, au sein même d'une population, il existe une corrélation positive entre les préférences des femmes pour les visages masculins et leur dégoût (sensibilité) face aux pathogènes (DeBruine, Jones et al. 2010).

ii. Quel compromis pour la féminité ?

Contrairement à la masculinité, il ne semble pas exister de compromis entre féminité et investissement chez les femmes. Par contre, il y a vraisemblablement un compromis entre féminité et performances physiques : à la puberté, la testostérone augmente la masse musculaire des jeunes hommes (Round 1999) ; les femmes ayant des taux élevés d'hormones masculines disposent de meilleures performances physiques que les femmes

avec un faible taux d'hormones masculines (Rickenlund, Carlström et al. 2003) ; et la prise d'androgènes augmente les capacités physiques (Shahidi 2001). Le compromis entre performances physiques et féminité est d'ailleurs extrême chez les sportives, dont le système hormonal est souvent perturbé (Rickenlund, Carlström et al. 2003; De Souza, Toombs et al. 2010). Une femme ayant un taux relativement élevé de testostérone (donc moins féminine), sera alors potentiellement plus performante, pour certaines tâches, qu'une femme plus féminine. Un certain degré de masculinité chez une femme peut donc être avantageux, et préféré par les hommes, dans certains environnements. Par exemple, une musculature relativement développée est nécessaire dans une société où les femmes participent à différentes tâches physiques (cueillette, agriculture, chasse, coupe de bois, construction, etc.). D'ailleurs, chez les chasseurs-cueilleurs Hadza en Tanzanie, les voix féminines (F0 élevée) sont associées à de moins bonnes compétences en récolte de nourriture par rapport à des voix plus masculines (Apicella & Feinberg 2009).

Ce compromis entre féminité et performances physiques est bien illustré par certaines pratiques culturelles. Par exemple, les corsets réduisaient considérablement le WHR des femmes qui les portaient (augmentant donc leur féminité), mais avaient également pour effet une forte limitation des capacités physiques. De même, le port des talons hauts par les femmes des sociétés occidentales actuelles modifie la posture de manière à augmenter la féminité (dont une réduction du WHR perçu), mais entraîne une réduction considérable de la mobilité (impossibilité de courir, de sauter ou encore de se battre) (Smith 1999).

La testostérone est également liée à certains traits comportementaux comme l'agressivité, la compétitivité ou l'assurance (Dabbs Jr, Ruback et al. 1988; Cashdan 1995; von der Pahlen, Lindman et al. 2002; Cashdan 2003). Ce type de comportements peut être

intéressant dans un milieu où, par exemple, le risque d'agression est élevé. D'autre part, le niveau de testostérone est positivement corrélé, chez les femmes, au niveau d'étude et au poste occupé (Purifoy & Koopmans 1979). Il est possible que les femmes ayant un taux plutôt élevé de testostérone présentent des caractéristiques de personnalité - comme la compétitivité ou l'assurance - qui facilitent certaines carrières (mais il existe aussi un effet de rétro-action, car les conditions de travail peuvent influencer la quantité d'hormones sécrétée). Même si le statut social est mieux connu pour influencer le succès reproducteur des hommes, il influence sans aucun doute celui des femmes.

Les variations géographiques et temporelles des préférences pour la féminité (dont le WHR), pourraient donc s'expliquer par l'intérêt relatif porté aux qualités reliées à la féminité (fertilité immédiate) par rapport aux caractéristiques liées à une certaine masculinité (performance physique, compétitivité, etc.), intérêt dépendant des conditions environnementales.

iii. Quel compromis pour la fertilité résiduelle ?

Nous avons montré dans cette thèse que l'attractivité féminine était en partie liée à la fertilité résiduelle, et que la préférence masculine pour ce trait était différente en France et en Indonésie. Il existe probablement un compromis pour la fertilité résiduelle expliquant cette différence.

La première hypothèse est l'existence d'un compromis entre fertilité résiduelle et fertilité immédiate. Dans le cas d'un tel compromis, les hommes pourraient privilégier les jeunes femmes ayant une fertilité immédiate élevée, au détriment de la fertilité résiduelle, dans un certain environnement, et préférer les jeunes femmes ayant une fertilité immédiate

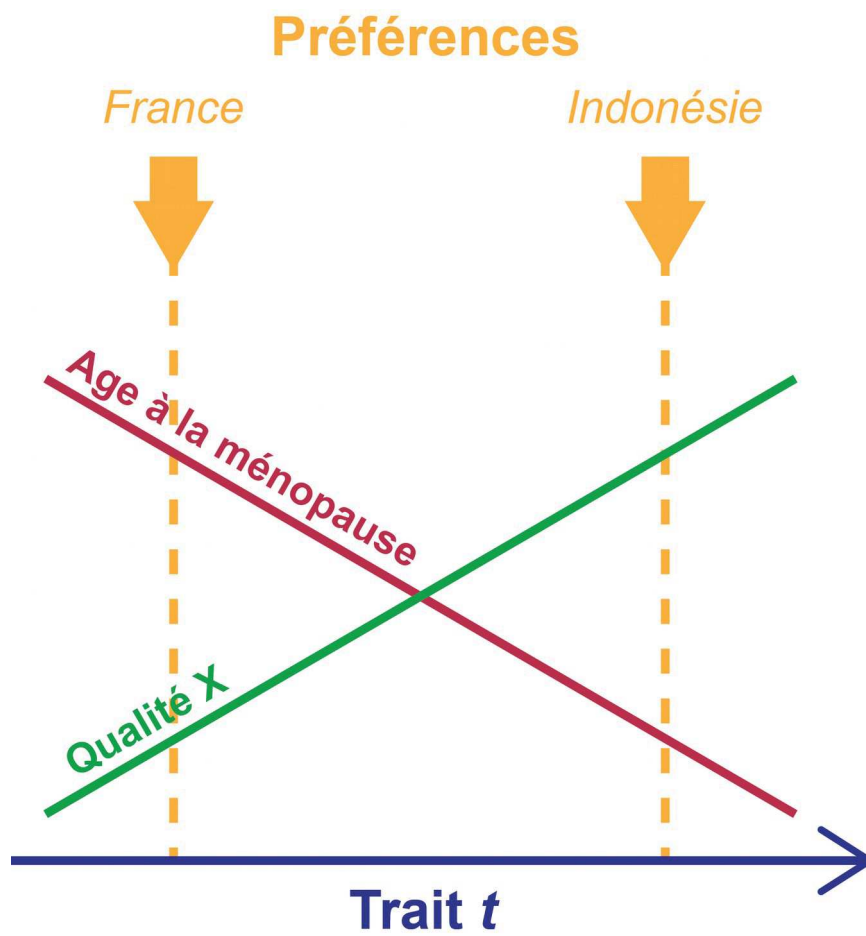


Figure 2. Illustration d'un mécanisme de compromis pouvant expliquer les différences de préférences observées entre la France et l'Indonésie. La qualité X et le trait du visage t restent à identifier.

moins importante mais disposant d'une plus grande fertilité résiduelle (âge à la ménopause élevé), dans un environnement différent. Il est envisageable que, dans un environnement présentant un fort taux de mortalité extrinsèque (due à un taux élevé de pathogènes par exemple), une préférence pour une femme pouvant avoir de nombreux enfants à un âge jeune soit plus avantageuse qu'une préférence pour une femme capable d'avoir des enfants sur une plus longue période. Cependant, aucune corrélation n'a été trouvée entre la fertilité immédiate des jeunes femmes (mesurée par les indices reliés au taux d'œstrogènes tels que la féminité du visage, le WHR, la hauteur de la voix), et leur fertilité résiduelle (mesurée par l'âge à la ménopause de la mère), ni en France ni en Indonésie (à notre connaissance cette corrélation n'existe pas non plus dans la littérature sur le sujet).

Supposons donc plutôt qu'il existe une qualité X (autre que la fertilité immédiate), négativement corrélée à l'âge à la ménopause, de telle manière que lorsque X augmente, l'âge à la ménopause diminue. En Indonésie, la qualité X pourrait être recherchée par les hommes, de telle sorte que les femmes signalant une haute valeur de X (grâce à un trait t du visage encore non identifié) sont jugées plus attirantes, même si leur reproduction cessera plus tôt. En France, les hommes préfèrent les femmes signalant une forte fertilité résiduelle (âge à la ménopause plus tardif), certainement au détriment de la qualité X qui serait alors moins importante dans notre environnement. Manifestement, les données manquent pour caractériser cette qualité X, ainsi que pour identifier les conditions environnementales favorisant les préférences masculines vers un côté ou l'autre de ce compromis *fertilité résiduelle/qualité X*.

La prochaine étape consistera à réaliser des tests d'attractivité croisés (visages d'Indonésiennes présentés à des juges français et inversement). Les résultats permettront de voir si la différence que nous avons observée provient bien d'une variation des préférences

masculines, ou bien s'il s'agit d'une variation de la signalisation de la fertilité résiduelle par les femmes entre les deux populations (avec une préférence masculine invariante). Dans ce dernier cas, les Français et les Indonésiens préféreraient la même valeur du trait t , mais le lien entre le trait t et l'âge à la ménopause serait différent dans les deux populations. Ensuite, il sera nécessaire d'identifier les caractéristiques du visage liées à la fertilité résiduelle qui sont utilisées par les hommes lors des jugements d'attractivité (le trait t). Cette étape donnera probablement des indices sur la nature de la qualité X. Pour ce faire, il est possible de réaliser un visage composite à partir de visages de femmes présentant un jeune âge à la ménopause, et un autre avec des femmes ayant une ménopause attendue plus tardive. Les différences entre les deux visages composites pourront fournir des indications sur le trait t .

I.3. Evolution des préférences au sein de sociétés en évolution

i. Des préférences plastiques

Durant cette thèse, nous avons étudié les variations des préférences entre époques, entre régions géographiques et entre individus. Il existe aussi des variations des préférences d'un même individu, qui traduisent une certaine plasticité des préférences. Nous avons vu que les préférences des femmes pour la masculinité variaient géographiquement en fonction du taux de pathogènes (Penton-Voak, Jacobson et al. 2004; DeBruine, Jones et al. 2010; DeBruine, Jones et al. 2011). Une étude a montré que la préférence d'une même femme pour la masculinité augmentait après une exposition à des images évoquant une présence de pathogènes (Little, DeBruine et al. 2011). Une autre preuve de la plasticité des

préférences se trouve chez les individus ayant émigré d'une population vers une autre, dans laquelle les préférences sont différentes. Ainsi, les personnes nées dans une société différente de celle d'origine de leurs parents ou grands-parents expriment généralement les mêmes préférences que les individus de la nouvelle population, dans laquelle ils sont nés. De plus, les personnes ayant changé de société pendant leur vie ont des préférences intermédiaires entre celles des populations d'origine et d'accueil (Tovee, Swami et al. 2006; Swami, Jones et al. 2009).

Par ailleurs, la perception des visages est modifiée par la présentation préalable d'autres visages. En effet, lorsque des participants sont soumis à un visionnage de visages présentant une configuration particulière, ils trouvent plus normaux et plus attirants qu'attendu les nouveaux visages présentant cette caractéristique (Rhodes, Jeffery et al. 2003; Rhodes, Jeffery et al. 2004; Leopold, Rhodes et al. 2005; Little, DeBruine et al. 2005). Par exemple, une habitude aux visages avec des traits expérimentalement élargis va faire paraître les nouveaux visages présentant des traits élargis plus normaux qu'avant l'habitude (Rhodes, Jeffery et al. 2003; Rhodes, Jeffery et al. 2004). Ce type d'effet résiduel (« after-effect » en anglais) pourrait refléter un recalibrage des préférences, afin qu'elles correspondent à la moyenne des individus récemment rencontrés. Cependant, il semblerait que ce recalibrage soit biaisé en faveur des caractéristiques communes aux visages attirants récemment rencontrés (Jones, DeBruine et al. 2008).

ii. Culture et médias

Cette plasticité en fonction des stimuli visuels récents a évidemment des conséquences importantes quant à l'influence des médias sur les préférences. En effet, les individus présentés dans les médias ne correspondent jamais tout à fait aux individus de la

population : ils sont, entre autres, généralement plus attirants que la moyenne de la population.

De fait, il existe un effet de l'exposition aux médias sur les préférences. Par exemple, après avoir observé des photos de jeunes femmes du magazine *Playboy*, les hommes jugent les photos de jeunes femmes « ordinaires » comme étant moins attirantes, et reportent moins d'attachement amoureux pour leur partenaire actuelle (Kenrick, Gutierrez et al. 1989). Au Salvador, les personnes ayant accès à internet préfèrent les hommes au visage plus masculin que les personnes sans accès internet (Batres & Perrett 2014). Sachant qu'au Salvador les conditions de santé sont moins bonnes dans les zones où internet est moins accessible, ce résultat est en contradiction avec le lien précédemment évoqué entre les préférences pour la masculinité et le taux de pathogènes. Il est cependant explicable par l'exposition aux médias (liés à internet), dans lesquels les hommes sont généralement plus masculinisés et les femmes plus féminisées que la moyenne. Dans cette étude, la préférence pour la féminité des visages de femmes était également plus forte pour les individus ayant accès à internet, ce qui peut s'expliquer par l'exposition aux médias, mais aussi par le compromis évoqué plus haut entre féminité et résistance à des conditions de vie difficiles (taux d'agression plus élevé dans les zones sans accès internet (Batres & Perrett 2014)).

Ainsi les médias, et plus généralement la culture, influencent les préférences. Mais les médias se basent sur les préférences. Par exemple, les femmes représentées dans les médias exhibent des caractéristiques qui, loin d'être arbitraires, ont un sens d'un point de vue adaptatif (critères de fertilité notamment). Dans un second temps, la surreprésentation de femmes attirantes dans les médias a, à son tour, des conséquences sur la perception de l'attractivité des individus de la population.

iii. Evolution des sociétés et préférences

Certaines modifications sociétales peuvent entraîner des modifications des conditions environnementales, qui peuvent potentiellement influencer les préférences. Prenons le cas de la transition démographique, définie par le passage d'une population ayant des taux de natalité et de mortalité élevés à une population ayant des taux de natalité et de mortalité faibles. Ainsi, dans les pays les plus développés, les taux de natalité sont aujourd'hui très faibles (transition démographique achevée). Il existe plusieurs théories sur la transition démographique (Borgerhoff Mulder 1998), et l'une d'entre elles suppose un changement de stratégie de reproduction. En effet, dans un environnement où la mortalité infantile est élevée, la stratégie optimale consiste à faire un grand nombre de descendants. A l'inverse, dans un environnement avec un faible taux de mortalité, où la probabilité de survie des enfants est plus élevée, il peut être avantageux de faire un petit nombre d'enfants afin de maximiser la quantité de ressources et d'investissement disponible pour chacun d'entre eux (Belsky, Steinberg et al. 1991). Il y a donc un compromis entre nombre et qualité des descendants (Lawson, Alvergne et al. 2012). Un indice de ce compromis a d'ailleurs été retrouvé durant cette thèse : le nombre de frères et sœurs est négativement corrélé à l'attractivité des jeunes filles, en France comme en Indonésie ($P < 0,01$). La transition démographique peut donc avoir un effet sur les préférences, puisque les conséquences de choisir une partenaire fertile ne seront pas les mêmes suivant que la stratégie optimale consiste à faire beaucoup de descendants ou peu de descendants plus compétitifs.

Ces changements démographiques sont récents, et les mécanismes physiologiques et psychologiques des populations modernes ne sont pas toujours adaptés aux nouvelles pressions évolutives. Par exemple, les préférences gustatives pour le sucre et les matières

grasses, qui ont été sélectionnées dans un environnement où ces nutriments étaient rares, sont maladaptatives dans certaines sociétés actuelles où les maladies liées à une surconsommation d'aliments gras et sucrés deviennent un problème de santé publique majeur. Un phénomène similaire pour les préférences dans le choix du partenaire ne peut pas être exclu, même si une certaine plasticité des préférences citée plus haut peut, dans une certaine mesure, contrer ce risque.

Notons que le fait que les préférences masculines varient dans le temps rend plus ardu l'interprétation des variations de ces préférences dans l'espace, et vice-versa. En effet, si l'on observe des préférences différentes entre deux zones géographiques, il peut s'agir d'une réponse à des facteurs locaux intrinsèquement différents (comme peut l'être la préférence pour une couleur de peau adaptée un ensoleillement local) ou d'une réponse à un événement similaire décalé dans le temps entre les deux régions (transition démographique). Connaître les préférences passées peut donc apporter des informations cruciales pour la compréhension des préférences actuelles. Cependant, comme nous avons pu le constater dans l'article 4, les moyens d'appréhender une variation temporelle de l'attractivité féminine sont limités. En effet, il est difficile d'évaluer de façon objective les critères d'attractivité du passé, car les traces écrites ne contiennent que des points de vue subjectifs, l'art pictural n'est pas toujours réaliste (la subjectivité de l'artiste peut transformer la réalité), et le véritable but d'une œuvre d'art (représenter la beauté, adopter ou transcender les normes d'un mouvement artistique, ou encore déranger une opinion contemporaine) n'est pas toujours clair.

I.4. Conclusion

Si l'on compare une femelle chimpanzé très courtisée et son équivalent chez *Homo sapiens*, on apprécie l'étendue de l'évolution en quelques millions d'années sur l'attractivité féminine. Si l'origine évolutive de certaines préférences masculines est évidente, d'autres critères d'attractivité sont plus complexes à appréhender.

Durant cette thèse, nous avons mis en évidence l'influence sur l'attractivité féminine de plusieurs caractéristiques physiques (WHR, traits du visage), correspondant à plusieurs « qualités » (fertilité immédiate, résiduelle) pouvant influencer le succès reproducteur de l'homme estimant cette attractivité. Les hommes utilisent des techniques différentes (vision directe ou périphérique) pour les détecter. Ces critères d'attractivité peuvent se situer sur une échelle *relative* à l'individu qui exprime la préférence (homogamie pour les traits neutres du visage), ou *absolue* (indices de fertilité). Néanmoins, même les traits situés sur une échelle *absolue* ne sont pas universaux, et nous avons pu observer que les préférences masculines varient géographiquement (traits du visage et fertilité résiduelle) et temporellement (WHR). Ces variations, même si elles sont inextricablement liées aux normes culturelles d'une société, sont loin d'être arbitraires. Les conditions environnementales (au sens large et incluant les caractéristiques sociétales) influencent les préférences, qui à leur tour ont des conséquences dans différents domaines de la société.

Nous sommes donc loin d'une unique beauté universelle et biologiquement fixée. L'étude des préférences dans le choix du partenaire s'avère complexe, car de nombreux paramètres non indépendants les uns des autres sont à prendre en compte (temporalité, localisation, culture, société, caractéristiques individuelles, ...). Malgré tout, l'attractivité

féminine peut s'étudier (donc se comprendre) en en considérant les compromis et les enjeux évolutifs, de la même manière que l'on peut expliquer les préférences gustatives par une imbrication de facteurs biologiques et socio-culturels, aux variations locales, temporelles et individuelles.

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Les éléments de l'attractivité féminine et leurs variations

Résumé : Dans le cadre du choix de partenaire, les préférences sont des mécanismes psychologiques permettant aux individus de choisir un (ou une) partenaire susceptible d'augmenter leur succès reproducteur. Comme le nombre de descendants d'un homme dépend largement de la fertilité de la (ou des) partenaire(s) qu'il choisit, la capacité à détecter et à préférer les femmes ayant une fertilité importante a été sélectionnée. Et puisque la fertilité d'une femme est en partie déductible de certaines caractéristiques physiques, l'attractivité féminine est en grande partie physique. Une approche expérimentale a été utilisée afin d'identifier les traits physiques influençant l'attractivité féminine, ainsi que les composantes de la fertilité desquelles ils sont les indices. En plus des indices connus de fertilité immédiate (c'est à dire la capacité d'une femme à engendrer un descendant à un moment donné), nos résultats montrent que les hommes sont également sensibles à des indices de fertilité résiduelle (nombre potentiel d'enfants qu'une femme pourra avoir dans le futur), partiellement définie par l'âge à la ménopause. Les moyens de détection de ces traits par les hommes ont également été analysés, démontrant l'importance de la vision périphérique lors de l'évaluation de l'attractivité d'un corps féminin. La question de l'universalité de ces critères d'attractivité a ensuite été abordée. Les différentes études montrent que les préférences masculines varient temporellement (la silhouette idéale, mesurée par le ratio taille/hanche, varie depuis le XVe siècle), géographiquement (les préférences pour la fertilité résiduelle diffèrent entre la France et l'Indonésie) et individuellement (on observe une préférence pour l'homogamie pour les traits du visage). Si nos résultats réfutent donc l'idée d'une beauté unique, universelle et biologiquement fixée, ces variations sont loin d'être arbitraires. Les variations des préférences s'expliquent par différents compromis et enjeux évolutifs, variant en fonction de conditions environnementales, culturelles, et individuelles.

Mots clés : Evolution, Homme, Choix de partenaire, Attractivité féminine, Fertilité, Ménopause, Compromis évolutifs, Visage, Ratio taille/hanche.

Women's attractiveness components and their variations

Abstract: In a context of mate choice, preferences are psychological mechanisms allowing individuals to choose a partner who can enhance their reproductive success. As a man's number of children greatly depends on the fertility of his mate(s), the ability to detect and prefer women with a high fertility has been selected. Moreover, as a woman's fertility is linked to various physical features, female attractiveness is largely physical. An experimental approach has been used to identify the physical traits influencing women's attractiveness, as well as the fertility characteristics of which they are the cues. In addition to well known cues of current fertility (i.e. a woman's ability to conceive a child at that given time), our results show that men are also sensitive to cues for residual fertility (i.e. the potential number of children a woman could have in the future), which is partially determined by age at menopause. Male means of detecting these features have been analysed too, highlighting the crucial role of the peripheral vision when judging the attractiveness of a woman's body. Furthermore, the issue of whether these attractiveness standards are universal has been addressed. Our studies show that men's preferences vary through time (the ideal body shape, determined by the waist-to-hip ratio, has changed since the 15th century), geographically (preferences concerning the residual fertility differ between France and Indonesia), and individually (a preference for homogamy has been found within facial features). Thus, our results disprove the notion of a single, universal and biologically fixed idea of beauty. But these variations of preferences are not arbitrary, and can be explained by evolutionary stakes and trade-offs, linked to environmental, cultural and individual conditions.

Keywords: Evolution, Human, Mate choice, Female attractiveness, Fertility, Menopause, Trade-offs, Face, Waist-to-hip ratio.