Contents lists available at ScienceDirect

Journal of Economic Psychology

journal homepage: www.elsevier.com/locate/joep

Adolescents gradually improve at detecting trustworthiness from the facial features of unknown adults



^a LaPsyDE (CNRS Unit 8240), Sorbonne – Université Paris Descartes, France

^b Toulouse School of Economics, France

^c Centre National de la Recherche Scientifique, Toulouse, France

A R T I C L E I N F O

Article history: Received 23 April 2014 Received in revised form 27 November 2014 Accepted 6 January 2015 Available online 14 January 2015

JEL classification: D81

PsycINFO classification: 3040

Keywords: Trust Adolescence Face Signal

ABSTRACT

People can (to some extent) detect trustworthiness from the facial features of social partners, and populations which underperform at this task are at a greater risk of abuse. Here we focus on situations in which adolescents make a decision whether to trust an unknown adult. Adolescents aged 13–18 (N = 540) played a trust game, in which they made decisions whether to trust unknown adults based on their picture. We show that trusting decisions become increasingly accurate with age, from a small effect size at age 13 to an effect size 2.5 times larger at age 18. We consider the implications of this result for the development of prosociality and the possible mechanisms underlying the development of trustworthiness detection from faces.

© 2015 Elsevier B.V. All rights reserved.

1. Introduction

The propensity to trust and cooperate is a central component of the human cognitive niche (Pinker, 2010; Whiten & Erdal, 2012). The problem with trusting easily, though, is that it makes one vulnerable to selfish agents willing to abuse trust (Fehr, 2009). Accordingly, people resort to various cognitive and social safeguards, which protect them against trusting the wrong persons. To decide whether to trust a given individual, people may rely on first-hand information about her trustworthiness, based on personal interactions (Chang, Doll, van't Wout, Frank, & Sanfey, 2010). In the absence of past personal interactions, they may rely on gossip and reputation (Laidre, Lamb, Shultz, & Olsen, 2013); and when there is no available record of the trustworthiness from facial features.

Indeed, convergent evidence suggests that healthy adults can discriminate, at least to some extent, between faces of cooperators and faces of abusers (Bonnefon, Hopfensitz, & De Neys, 2013; De Neys, Hopfensitz, & Bonnefon, 2013; Little & Jones, 2013; Stirrat & Perrett, 2010; Tognetti, Berticat, Raymond, & Faurie, 2013; Yamagishi, Tanida, Mashima, Shimoma, & Kanazawa, 2003). Without this capacity to read trustworthiness from faces, people would be at a greater risk of abuse. And indeed, recent research linked older adults' greater vulnerability to fraud, to a diminished capacity to read trustworthiness





CrossMark

^{*} Corresponding author at: CLLE, Maison de la recherche, 5 allées A. Machado, 31058 Toulouse Cedex 9, France. Tel.: +33 5 61 50 36 01. *E-mail address:* bonnefon@univ-tlse2.fr (J.-F. Bonnefon).

from faces (Castle et al., 2012). This diminished capacity was correlated with a muted response of the anterior insula, suggesting that older adults lacked a proper "gut response" to untrustworthy faces.

In this article, we focus on another period of heightened vulnerability to abuse, adolescence. During their transition to autonomous decision-making, teenagers have many opportunities to interact with unknown adults in novel contexts, and these interactions may involve decisions to trust or not to trust unknown adults. We already know from behavioral economic experiments that adolescents become increasingly trusting (Sutter & Kocher, 2007; Van den Bos, van Dijk, & Crone, 2012; Van den Bos, Westenberg, van Dijk, & Crone, 2010). However, as emphasized by Evans, Athenstaedt, and Krueger (2013), we do not know whether this growing propensity to trust goes together with an increased performance at trusting the right person. In parallel, we already know that young children can show adult-like levels of consistency in their judgments of facial trustworthiness (Cogsdill, Todorov, Spelke, & Banaji, 2014), but we do not know whether these judgments, consistent as they are, are also accurate.

In sum, it is an important, unanswered question whether or when adolescents can reliably detect trustworthiness from adult faces. To answer this question, we conducted a study where 540 participants aged 13 to 18 played a classic trust game, in which they made decisions whether to trust adults based on their facial features. We recorded the accuracy of these decisions in order to track the developmental trajectory of trustworthiness detection from adult faces.

2. Disclosure statement

We report all measures, conditions, and data exclusions. The sample size for the study was exogenously determined as the highest possible number of volunteers in the two schools we contacted.

3. Method

3.1. Participants

The study took place in two suburban secondary schools in Belgium. After excluding 15 participants for not reporting their age or for being outside of our target age range (13–18), the data for 540 participants were retained for analysis. Table 1 shows the breakdown of these participants, by gender and age.

3.2. Procedure

The study was conducted on the school premises. Participants sat in front of individual computers, and were told about the rules of the 14-round trust game they were about to play, in the role of Investor, with 14 different adult Trustees. Note that while the words 'Investor' and 'Trustee' are used for clarity here, they were never actually used in the experiment. The Trustee was simply called 'the other player'.

Each round had the same structure: Participants were endowed with an hypothetical sum of 4 euros (all payoffs were hypothetical, as requested by the school boards) and had to decide whether to keep the endowment, or to transfer that endowment to a Trustee, whose picture appeared on the screen. In case the endowment was transferred, it was multiplied by three, and the Trustee had to decide whether to keep the whole 12 euros, to return 6 euros to the Investor, or to return 4 euros to the Investor. We refer to these strategies as the Abuser, Cooperator, and Neutral strategies, respectively. These terms were not mentioned to the participants. The participants were informed that each Trustee had already recorded his or her strategy. Because the school boards were opposed to incentivizing the students, the payoffs were only hypothetical.

Each round started with a fixation cross (1000 ms), followed by the picture of the Trustee (5500 ms). Pictures were presented in randomized order for each participant. Participants indicated whether they wanted to transfer money to the Trustee by pressing one of two keys, after which they moved on to the next round, without receiving feedback about the strategy of the Trustee.

After having played the 14 rounds, participants were asked for an estimate of the overall proportion of Trustees that they believed would return nothing (the Abuser strategy). This question was meant to capture their explicit beliefs about trust-worthiness, as compared to the implicit judgments captured by their decisions during the game. Finally, participants indicated what would have been their own strategy had they played Trustee: keep 12 (Abuser), keep 8 (Neutral), or keep 6 (Cooperator). Eight participants did not record their responses to either or both of these questions. A subset of participants also recorded their birth order among their siblings, but this measure was not used in any analysis.

3.3. Materials

Most importantly, the Trustees shown to the participants had recorded their strategy in the context of a previous study (Centorrino, Djemai, Hopfensitz, Milinski, & Seabright, in press). In this initial study, 84 young adults played the role of Trustee, and recorded a movie introducing themselves. From each of these movies, a research assistant blind to the strategies of the Trustees extracted one frame in which the Trustee had the most neutral expression. Each picture was then cropped (left and right facial boundaries, chin and top of the eyebrows) to minimize display of clothing or hairstyle, and turned to black and white (see Fig. 1). A set of 60 of these pictures was used for the trustworthiness detection studies reported in

Table	1
-------	---

General statistics, broken down by age.

Age	13	14	15	16	17	18
Number of boys	40	40	40	46	45	37
Number of girls	46	41	57	52	36	60
% of transfer from teenagers	44	44	44	45	45	45
Teenage estimation of % of adult abusers	43	48	45	45	44	44
% of teenage cooperators	33	40	35	42	40	37
% of teenage abusers	13	21	16	10	10	12



Fig. 1. Mock example of the pictures used in the experiment. Black and white version of the faces are cropped at the left and right facial boundaries, chin and top of the eyebrows.

Bonnefon et al. (2013). Because it was not feasible to run 60 rounds in the current study, we selected a subset of 14 pictures: 6 pictures of Abusers (3 males, 3 females), 2 pictures of Neutral players as fillers (1 male, 1 female), and 6 pictures of Cooperators (3 males, 3 females). Because the current study investigates a negative moderator (age) of the original trustworthiness detection effect, we maximized power by selecting pictures of Cooperators and Abusers that were highly discriminated in our original studies conducted in an adult population. That is, we selected the 3 male Cooperators and 3 female Cooperators who were best discriminated as such in previous studies, and the 3 male Abusers and 3 female Abusers who were best discriminated as such in previous studies.

4. Results

As shown in Table 1, age on its own had no effect on the proportion of transfer decisions, on the estimation of the proportion of Abusers among the Trustees, or on the participants' own hypothetical strategy as Trustee.

4.1. Trustworthiness detection

Fig. 2A displays the probability of transferring to Cooperators and Abusers, as a function of age. It suggests that the discrimination between Cooperators and Abusers improves regularly with age. We conducted a repeated-measure analysis of covariance, with the probability of transfer to the Trustee as the dependent measure, in which the strategy of the Trustee was entered as a 2-level factor, the gender of the participant as a grouping variable, and the age of the participant as a covariate. Gender and age had no effect on their own, F = 1.0, p > .30 (all significance tests reported in this article are two-tailed). The strategy of the Trustee had a detectable main effect, F(1,537) = 4.0, p = .05; but most importantly, this effect was qualified by the expected interaction with age, F(1,537) = 10.9, p < .001.

Signal Detection Theory provides a useful measure of trustworthiness detection in the form of the sensitivity index *d'*, which can be used in this setting to estimate the discriminability of Cooperators in the different age groups. For each participant, we computed:

$$d' = Z(T_C) - Z(T_A),$$

where T_c is the proportion of trusting decisions when playing with Cooperators, T_A is the proportion of trusting decisions when playing with Abusers, and *Z* returns the inverse of the standard normal cumulative distribution.¹

The discrimination of Cooperators increased from d' = .22 at age 13 (41% transfer to Abusers, 48% transfer to Cooperators), to d' = .55 at age 18 (36% transfer to Abusers, 56% transfer to Cooperators). Even at age 13, participants transferred more to Cooperators than to Abusers, t(85) = 2.6, p = .01, but the effect size was 2.5 times as large at age 18 than at age 13.

¹ Note that d' is undefined when the proportion of trusting decisions is 0 or 1. Following convention, we replaced proportions of 0 and 1 with $\frac{1}{12}$ and $1 - \frac{1}{12}$, respectively, in which 12 is the total number of trusting decisions made by a participant (excluding the two filler pictures which do not enter in the sensitivity computation).



Fig. 2. Main experimental results. Error bars show the standard error of the mean. (A) Probability of transfer to Cooperators and Abusers: The discrimination between Cooperators and Abusers improves with age. (B) Estimated proportion of Abusers: The older the participants, the more they follow social projection and believe that others behave the same as themselves.

Interestingly, the analysis of covariance also detected an interaction between the strategy of the Trustee and the gender of the participant, F(1, 537) = 7.9, p < .01. This interaction reflects the fact that the strategy of the Trustee had a greater impact on girls than it had on boys. Furthermore, this greater impact went in the direction of better performance. Indeed, Girls (d' = .49) appeared to be better trustworthiness detectors than boys (d' = .30). This result must be interpreted carefully, though, since the number of girls and boys was imbalanced (60 vs. 37) in the best performing age group (18 yo).

4.2. Additional results

At the end of the experiment, we asked participants to provide an explicit estimate of the proportion of Trustees whose strategy was to abuse trust. In the series of games they just played, the actual proportion was 43%, and on average participants did believe the proportion to be about 45%. Their response, though, depended on an interesting yet unpredicted mixture of age and social projection.

Fig. 2B displays the estimated proportion of Abusers, as a function of participants' age and own strategy as Trustee. Younger participants estimated the proportion of Abusers at about 45%, independently of their own strategy. Older participants, though, were influenced by their own strategy. Would-be Cooperators thought that only 33% of people were Abusers, whereas would-be Abusers thought that about 67% of people were Abuser. Would-be neutral players fell somewhere in between.

An analysis of covariance confirmed this result, in which the estimated proportion of Abusers was entered as the dependent variable, the participant's own hypothetical strategy as a random factor, and the age of the participant as a covariate. Age did not have an effect of its own, F(1,526) = 3.2, p = .08. The analysis detected an effect of strategy, F(2,526) = 6.6, p = .001, but this effect was qualified by the expected interaction with age, F(2,526) = 8.6, p < .001. Older participants were more likely than younger participants to project their own strategy on others.

Note that this effect only concerned participants' explicit beliefs about trustworthiness, and not the implicit trustworthiness judgments reflected in the decisions they made in the game. To confirm that dissociation, we ran an analysis of covariance in which the proportion of decisions to transfer was entered as the dependent variable, the participant's own hypothetical strategy as a random factor, and the age of the participant as a covariate (i.e., the same analysis as above except for the dependent variable). This analysis did not detect any significant main effect or interaction effect, all F < 1.8, all p > .16.

5. Discussion

We tracked teenagers' performance at detecting trustworthiness from the faces of young adults, and we observed that their performance gradually improved with age. Although they already performed better than chance at age 13, the effect size was 2.5 times larger at age 18.

In addition to this main result, we observed that teenage girls seemed to be better trustworthiness detectors than teenage boys. Finally, we observed that while the trusting decisions of participants got more accurate with age, their explicit judgments about trustworthiness did not. While older participants trusted better in the game, their explicit judgments increasingly deviated in the direction of social projection. That is, they increasingly assumed that Trustees followed the same strategy that they would choose as their own, a result already reported for adult players (Glaeser, Laibson, Scheinkman, & Soutter, 2000; Sapienza, Toldra-Simats, & Zingales, 2013).

This dissociation (increasingly accurate decisions but increasingly inaccurate judgments) is consistent with the current hypothesis that reading trustworthiness from faces is an intuitive process, or a "gut response" (Bonnefon et al., 2013; Castle et al., 2012). Trustworthiness detection is not always accurate (Efferson & Vogt, 2013; Vogt, Efferson, & Fehr, 2013), and it is in fact better when information is limited or participants are distracted (Manson, Gervais, & Kline, 2013; Reinhard, Greifeneder, & Scharmach, 2013; Sylwester, Lyons, Buchanan, Nettle, & Roberts, 2012). That is, trustworthiness detection appears to improve when people do not consciously try to assess trustworthiness. As a result, the actual decisions whether to trust unknown individuals are more accurate than the explicit beliefs about whether unknown individuals are trustworthy (Bonnefon et al., 2013). The present data further support this hypothesis. In particular, even though very young children are quite consistent in their explicit judgments about whether an adult face is trustworthy (Cogsdill et al., 2014), the present data entail that their judgments are unlikely to be accurate until late adolescence. This disparity suggests that explicit impressions of trustworthiness from faces are largely biased (Olivola, Funk, & Todorov, 2014), from an early age, whereas actual decisions to trust based on facial features acquire a kernel of accuracy in later years.

The present data also have interesting implications for understanding the development of trust and prosociality during adolescence (Sutter & Kocher, 2007; Van den Bos et al., 2012, 2010). If adolescents get better at reading trustworthiness from adult faces, their decisions to trust adults are increasingly likely to be positively reinforced. Since trust can quickly build up when it is rewarded (e.g., Fetchenhauer & Dunning, 2010), it is reasonable to expect that adolescents would become more trusting as a result of becoming better trustworthiness detectors, over and above any additional effect of social projection on cooperation (Kruger, 2013).

The main question raised by our data, though, concerns the mechanisms that drive the gradual improvement of the ability to detect trustworthiness from adult faces during adolescence. At this stage, we can consider three potential accounts: the gradual acquisition of a general capacity to detect trustworthiness from faces; an increased proximity to the age group to which the Trustees belong; and an increased exposure to peers with stable facial features. We now consider in turn these three possibilities, then the testable predictions they afford.

First, it is unlikely that the developmental trend we observed simply reflects the development of cognitive capacity in general. Indeed, Bonnefon et al. (2013) showed that trustworthiness detection from faces was neither correlated with cognitive capacity, nor impaired by concurrent cognitive load. Yet, it is possible that trustworthiness detection from faces requires a degree of expertise in facial processing which is only reached during adolescence. The sensitivity to differences in the spacing of facial features develops for the most part during the preschool years, but it can be refined until adolescence (Mondloch, Le Grand, & Maurer, 2010). Accordingly, the development of trustworthiness detection from faces may reflect late and subtle developments in facial processing.

Second, we know from research on face recognition that people are better at identifying faces that correspond to their own age group, an effect called the own-age bias: Children recognize children's faces better, and adults recognize adult faces better (Anastasi & Rhodes, 2005; Hills & Lewis, 2011). This effect appears to result from repeated exposure to the faces of same-age peers, and can be canceled by repeated exposure to another age group: Trainee teachers, for example recognize children faces faster and as accurately as adult faces (Harrison & Hole, 2009). To the extent that facial recognition may result in an advantage for facial trustworthiness detection (an assumption which would need closer scrutiny), our results could reflect the decreasing distance between the age of the participants and that of the Trustees.

Third, detecting trustworthiness from faces presumably requires the brain to track some form of correlation between facial features and cooperative behavior. A potential problem for tracking this correlation is that facial features are highly unstable during adolescence – their geometry does not stabilize until age 16 for girls, and even later for boys (Bulygina, Mitteroecker, & Aiello, 2006; Coquerelle et al., 2011). In the age-segregated societies typically found in Western cultures, children and adolescents mostly interact with individuals who are within one or two years of their own age (Konner, 2010), which would deny them the opportunity to track a correlation between facial features and cooperative behavior, since individuals in their peer group have unstable facial features. Accordingly, our results could reflect an increased exposure to the behavior of individuals whose facial features are stable.

These three accounts afford different testable predictions regarding the ability of adults and adolescents to detect trustworthiness on adult and adolescent faces. The first account (gradual deployment of a general capacity) would predict that adults can detect trustworthiness from faces of all age groups, whereas young adolescents cannot (or much less so). The second account (own-age bias) would predict that adults are better at detecting trustworthiness from adult faces, whereas young adolescents are better at detecting trustworthiness from young adolescents' faces. The third account (exposure to stable faces) would predict that adults can only detect trustworthiness from adult faces, whereas adolescent do not perform well either from adult or young adolescent faces. Testing the three accounts would accordingly require a large scale study, four times larger than the current one, that would measure trustworthiness detection by adults and adolescents, from adult and adolescent faces.

6. Author note

AH, JFB and WDN designed the research; WDN conducted the study; JFB and WDN analyzed the data; AH, JFB and WDN wrote the article

Acknowledgement

Thanks to Claudia Verlinden and Eline Raedschelders for their help in running the experiments. AH gratefully acknowledges support through the Institute of Advanced Studies Toulouse (IAST) and financial support through ANR Grant 2010 JCJC-180301.

References

Anastasi, J. S., & Rhodes, M. G. (2005). An own-age bias in face recognition for children and older adults. *Psychonomic Bulletin & Review*, 12, 1043–1047. Bonnefon, J. F., Hopfensitz, A., & De Neys, W. (2013). The modular nature of trustworthiness detection. *Journal of Experimental Psychology: General*, 142, 143–150.

Bulygina, E., Mitteroecker, P., & Aiello, L. (2006). Ontogeny of facial dimorphism and patterns of individual development within one human population. American Journal of Physical Anthropology, 131, 432–443.

Castle, E., Eisenberger, N. I., Seeman, T. E., Moons, W. G., Boggero, I. A., Grinblatt, M. S., et al (2012). Neural and behavioral bases of age differences in perceptions of trust. Proceedings of the National Academy of Science of the USA, 109, 20848–20852.

Centorrino, S., Djemai, E., Hopfensitz, A., Milinski, M., Seabright, P. (in press). Honest signalling in trust interactions: Smiles rated as genuine induce trust and signal higher earnings opportunities. Evolution and Human Behavior.

Chang, L. G., Doll, B. B., van't Wout, M., Frank, M. J., & Sanfey, A. G. (2010). Seeing is believing: Trustworthiness as a dynamic belief. Cognitive Psychology, 61, 87–105.

Cogsdill, E. J., Todorov, A. T., Spelke, E. S., & Banaji, M. R. (2014). Inferring character from faces: A developmental study. *Psychological Science*, 25, 1132–1139. Coquerelle, M., Bookstein, F. L., Braga, J., Halazonetis, D. J., Weber, G., & Mitteroecker, P. (2011). Sexual dimorphism of the human mandible and its association with dental development. *American Journal of Physical Anthropology*, 145, 192–202.

De Neys, W., Hopfensitz, A., & Bonnefon, J. F. (2013). Low second-to-fourth digit ratio predicts indiscriminate social suspicion, not improved trustworthiness detection. *Biology Letters*, 9, 20130037.

Efferson, C., & Vogt, S. (2013). Viewing men's faces does not lead to accurate predictions of trustworthiness. *Scientific Reports*, 3. http://dx.doi.org/10.1038/ srep01047.

Evans, A. M., Athenstaedt, U., & Krueger, J. I. (2013). The development of trust and altruism during childhood. *Journal of Economic Psychology*, 36, 82–95. Fehr, E. (2009). On the economics and biology of trust. *Journal of the European Economics Association*, 7, 235–266.

Fetchenhauer, D., & Dunning, D. (2010). Why so cynical? Asymmetric feedback underlies misguided skepticism regarding the trustworthiness of others. *Psychological Science*, 21, 189–193.

Glaeser, E. L., Laibson, D. I., Scheinkman, J. A., & Soutter, C. L. (2000). Measuring trust. Quarterly Journal of Economics, 115, 811–846.

Harrison, V., & Hole, G. J. (2009). Evidence for a contact-based explanation of the own-age bias in face recognition. Psychonomic Bulletin & Review, 16, 264–269.

Hills, P. J., & Lewis, M. B. (2011). The own-age face recognition bias in children and adults. Quarterly Journal of Experimental Psychology, 64, 17-23.

Konner, M. (2010). The evolution of childhood: Relationships, emotion, mind. Cambridge, MA: Harvard University Press.

Kruger, J. I. (2013). Social projection as a source of cooperation. *Current Directions in Psychological Science*, 22, 289–294.

Laidre, M., Lamb, A., Shultz, S., & Olsen, M. (2013). Making sense of information in noisy networks: Human communication, gossip, and distortion. Journal of Theoretical Biology, 317, 152–160.

Little, A., & Jones, B. (2013). Accuracy in discrimination of self-reported cooperators using static facial information. Personality and Individual Differences, 54, 507–512.

Manson, J. H., Gervais, M. M., & Kline, M. A. (2013). Defectors cannot be detected during "small talk" with strangers. PloS one, 8, e82531.

Mondloch, C., Le Grand, R., & Maurer, D. (2010). Development of expertise in face recognition. In I. Gauthier, M. J. Tarr, & D. Bub (Eds.), Perceptual expertise: Bridging brain and behavior (pp. 67–106). Oxford: Oxford University Press.

Olivola, C. Y., Funk, F., & Todorov, A. (2014). Social attributions from faces bias human choices. *Trends in Cognitive Sciences*, 18, 566–570.

Pinker, S. (2010). The cognitive niche: Coevolution of intelligence, sociality, and language. Proceedings of the National Academy of Sciences of the USA, 107, 8993–8999.

Reinhard, M. A., Greifeneder, R., & Scharmach, M. (2013). Unconscious processes improve lie detection. Journal of Personality and Social Psychology, 105, 721–739.

Sapienza, P., Toldra-Simats, A., & Zingales, L. (2013). Understanding trust. The Economic Journal, 123, 1313–1332.

Stirrat, M., & Perrett, D. (2010). Valid facial cues to cooperation and trust: Male facial width and trustworthiness. Psychological Science, 21, 349-354.

Sutter, M., & Kocher, M. G. (2007). Trust and trustworthiness across different age groups. Games and Economic Behavior, 59, 364–382.

Sylwester, K., Lyons, M., Buchanan, C., Nettle, D., & Roberts, G. (2012). The role of theory of mind in assessing cooperative intentions. Personality and Individual Differences, 52, 113–117.

Tognetti, A., Berticat, C., Raymond, M., & Faurie, C. (2013). Is cooperativeness readable in static facial features? An intercultural approach. Evolution and Human Behavior, 34, 427-432.

Van den Bos, W., van Dijk, E., & Crone, E. A. (2012). Learning whom to trust in repeated social interactions: A developmental perspective. Group Processes & Intergroup Relations, 15, 243–256.

Van den Bos, W., Westenberg, P. M., van Dijk, E., & Crone, E. A. (2010). Development of trust and reciprocity in adolescence. Cognitive Development, 25, 90-102.

Vogt, S., Efferson, C., & Fehr, E. (2013). Can we see inside? Predicting strategic behavior given limited information. Evolution and Human Behavior, 34, 258–264.

Whiten, A., & Erdal, D. (2012). The human socio-cognitive niche and its evolutionary origins. *Philosophical Transactions of the Royal Society B*, 367, 2119–2129.

Yamagishi, T., Tanida, S., Mashima, R., Shimoma, E., & Kanazawa, S. (2003). You can judge a book by its cover: Evidence that cheaters may look different from cooperators. *Evolution and Human Behavior*, 24, 290–301.