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WHEN WILL THE FITTEST SURVIVE? -AN INDIRECT EVOLUTIONARY ANALYSIS-

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When will the fittest survive? - An indirect evolutionary analysis -

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Abstract

Survival of the fittest means that phenotypes behave as if they would maximize reproductive success. An indirect evolutionary analysis allows for stimuli which are not directly related to reproductive success although they affect behavior. One first determines the solution for all possible constellations of stimuli and then the evolutionarily stable stimuli. Our general analysis confirms the special results of former studies that survival of the fittest in case of commonly known stimuli requires either that own success does not depend on other's behavior or that other's behavior is not influenced by own stimuli. When stimuli are private information one can derive similar necessary conditions for the survival of the fittest.

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1. Introduction

As in evolutionary biology evolutionary game theory (see the survey of Hammerstein and Selten, 1994) assumes genetically determined behavior and tries to determine the evolutionarily stable genotype or behavior. Whereas this makes sense for primitive organisms like plants, the assumption of genetically determined behavior is impossible for more highly developed species since they live in complex environments and therefore face far too many different choice problems.

The basic idea of the indirect evolutionary approach, as initiated by Güth and Yaari (1992), is to allow for an indirect dependence of behavior on genetically determined stimuli. More specifically, it is assumed that genetically determined stimuli define a game which one has to solve in order to derive how behavior depends on these genetically determined stimuli - we refer to this as the first step of an indirect evolutionary analysis. Although we rely on rationality as most of the previous studies do, it would be even more important to apply psychologically more convincing ideas when solving the game (see Güth and Kliemt, 1996, for a first and still unsatisfactory attempt).

By inserting the solution into the material payoff function one then knows how (reproductive) success depends indirectly on genetically determined stimuli via the solution of the game. This defines an evolutionary game whose strategies are the genetically determined stimuli. Like in usual evolutionary game theory the second step of an indirect evolutionary analysis requires to determine the evolutionarily stable strategy or stimuli. If stimuli are private information, behavior can, of course, depend only on the beliefs about the stimuli of others.

Previous studies (e.g. Bester and Güth, forthcoming, Güth, 1995, Güth and Huck, 1995, Güth and Kliemt, 1995) invariantly proved the following type of results for the case of commonly known stimuli: Survival of the fittest (in the sense of maximizing reproductive success) results if

(I.i) own success does not depend on other players' behavior

(I.ii) own stimuli do not influence other players' behavior where it may suffice if these conditions are true only locally. Furthermore, it has been argued that (I.ii) also covers the result of privately known stimuli which cannot be signaled at all.

The purpose of this study is to prove that such results are generally true, i.e. independent of the specific context. We first demonstrate this in section 2 for the simplest case where both the commonly known stimuli and the strategies are one-dimensional. A simple example of pollution by production is used in section 3 to illustrate our general findings. In section 4 it is shown how the results can be generalized for multi-dimensional situations as well as for more refined solution concepts. Section 5 introduces a narrow class of Bayesian games for which symmetric Bayesian equilibria exist. Then, in section 6 the evolutionarily stable distribution is analysed before, finally, section 7 concludes with an extension of the analysis of the example to privately known stimuli.

Quite often the results of indirect evolution resemble those of the literature on commitment in interactive decision making, e.g. in agency relationships (see, for instance, van Damme and Hurkens, 1996, who also review some of this literature). There are, however, important differences of the two approaches: Strategic commitment relies on an overall game model whereas in indirect evolution no decision maker has to be aware of the evolutionary forces, i.e. the modelling tasks are very different. As will demonstrated below indirect evolution allows to distinguish between utility and (reproductive) success what in strategic delegation requires different agents, e.g. by modelling a firm as a team of a principal and an agent when analysing strategic commitment of competing firms (see Dufwenberg and Güth, 1997).

2. The one-dimensional case with commonly known stimuli

Let S, with $S \subset \mathbb{R}$, be a closed interval with a non-empty interior. An element s_i of S is a strategy or a form of behavior of player i. Similarly, let M with $M \subset \mathbb{R}$ be a closed interval whose non-empty interior contains 0. The elements $m_i \in M$ are the genetically determined stimuli which, together with the chosen strategies, determine the payoff $H_1(s_1, s_2; m_1, m_2)$ of the symmetric 2 person-game

(II.1) $G(m_1, m_2) = (S; H_1(s_1, s_2; m_1, m_2))$

for all $m_1, m_2 \in M$ where, of course, symmetry implies that player 2's payoff function is determined by

(II.2) $H_2(s_1, s_2; m_1, m_2) = H_1(s_2, s_1; m_2, m_1)$.

We assume that $H_1(s_1, s_2; m_1, m_2)$ is continuous in all its arguments and quasi-concave in s_1 for all $s_2 \in S$ and $m_1, m_2 \in M$. Furthermore, let the constellation $(m_1, m_2) \in M \times M$ be common knowledge. From these assumptions (see, for instance, van Damme, 1987) it follows

Remark 1: *For all $m_1, m_2 \in M$ game $G(m_1, m_2)$ has at least one equilibrium*

$$s^*(m_1, m_2) = (s_1^*(m_1, m_2), s_2^*(m_1, m_2)).$$

An obvious implication of the symmetry of $G(m_1, m_2)$ in the sense of (II.2) is

Lemma 2: *For all $m_1, m_2 \in M$ and all equilibria $s^* = (s_1^*, s_2^*)$ of $G(m_1, m_2)$ the strategy vector (s_2^*, s_1^*) is an equilibrium of $G(m_2, m_1)$.*

Proof. From (II.2) and the best reply property for player 2 it follows that

$$\begin{aligned} H_1(s_2^*, s_1^*; m_2, m_1) &= H_2(s_1^*, s_2^*; m_1, m_2) \geq \\ H_2(s_1^*, s_2; m_1, m_2) &= H_1(s_2, s_1^*; m_2, m_1) \end{aligned}$$

for all $s_2 \in S$ as required. ■

Although the indirect evolutionary approach can be applied also by relying on equilibrium selection (see Güth and Nitzan, forthcoming), we circumvent this problem by requiring

Uniqueness: *For all $m_1, m_2 \in M$ the game $G(m_1, m_2)$ has only one equilibrium $s^*(m_1, m_2) = (s_1^*(m_1, m_2), s_2^*(m_1, m_2))$ to which we refer as the solution of $G(m_1, m_2)$.*

Uniqueness of $s^*(m_1, m_2)$ for all $m_1, m_2 \in M$ and upper hemicontinuity of the set of equilibria (Fudenberg and Tirole, 1991) implies

Remark 3: *The solution strategies $s_i^*(m_1, m_2)$ are continuous in $m_1, m_2 \in M$.*

Since the second step of indirect evolutionary analysis, namely the derivation of evolutionarily stable stimuli, will be based on differentiability, it is important to investigate the differentiability of the solution strategy $s_i^*(m_1, m_2)$. In order to do so we introduce the following Assumption.

Interiority: *For all $m_1, m_2 \in M$ the Nash equilibria of $G(m_1, m_2)$ are interior points of $S \times S$.*

Lemma 4: *Assume that $H_1 = H_1(s_1, s_2; m_1, m_2)$ has the following properties:*

(i) *$H_1(s_1, s_2; m_1, m_2)$ is concave in s_1 for every $s_2 \in S$ and $m_1, m_2 \in M$;*

(ii) *$H_1(s_1, s_2; m_1, m_2)$ is three times continuously differentiable in s_1, s_2, m_1 and m_2;*

(iii) *the Jacobian*

$$\begin{vmatrix} \frac{\partial^2}{\partial s_1^2} H_1 & \frac{\partial^2}{\partial s_1 \partial s_2} H_1 \\ \frac{\partial^2}{\partial s_1 \partial s_2} H_2 & \frac{\partial^2}{\partial s_2^2} H_2 \end{vmatrix} \neq 0$$

for all $s_1, s_2 \in int\ (S)$ and $m_1, m_2 \in int(M)$.

Under the foregoing assumptions the (symmetric) strategies $(s_1^*(m_1, m_2), s_2^*(m_1, m_2))$ are twice continuously differentiable in m_1 and m_2 (on int (M)).

Proof. Let $m_1, m_2 \in \text{int } (M)$. By Uniqueness, Interiority, (i), and (ii), the equilibrium $(s_1^*(m_1, m_2), s_2^*(m_1, m_2))$ is the unique (interior) solution of the following equations:

$$\begin{aligned} \frac{\partial}{\partial s_1} H_1(s_1, s_2; m_1, m_2) &= 0 \\ \frac{\partial}{\partial s_2} H_2(s_1, s_2; m_1, m_2) &= 0 \end{aligned}$$

Now, by (ii), (iii), and the Implicit Functions Theorem, $s_i^*(m_1, m_2)$ for $i = 1, 2$ is twice continuously differentiable. ■

Another result is

Lemma 5: $s_1^*(m_1, m_2) = s_2^*(m_2, m_1)$ *for all $m_1, m_2 \in M$.*

Proof. Let $(s_1^*(m_1,m_2), s_2^*(m_1,m_2))$ be the solution of $G(m_1,m_2)$. According to Lemma 2 the strategy vector $(s_2^*(m_1,m_2), s_1^*(m_1,m_2))$ is an equilibrium of $G(m_2,m_1)$. Thus uniqueness of the solution for $G(m_2,m_1)$ implies $s_2^*(m_2,m_1) = s_1^*(m_1,m_2)$. ∎

The first step of an indirect evolutionary analysis amounts to compute $s^*(m_1,m_2) = (s_1^*(m_1,m_2), s_2^*(m_1,m_2))$ for all games $G(m_1,m_2)$ with $m_1,m_2 \in M$. Having completed this task the second step starts with the definition of the evolutionary game

(II.3) $\Gamma = (M; M; R_1(m_1,m_2), R_2(m_1,m_2))$

(II.4) $R_i(m_1,m_2) = H_i(s^*(m_1,m_2); \lambda m_1, \lambda m_2)$ for $i = 1,2$.

Here λ measures how stimuli are directly related to (reproductive) success $R_i(m_1,m_2)$ where we allow only for the two extreme relationships $\lambda = 0$, i.e. stimuli influence success only indirectly via $s^*(m_1,m_2)$, and $\lambda = 1$ where stimuli are directly related to (reproductive) success.

Thus the set M of possible, genetically determined stimuli is the strategy set of both players $i = 1,2$. The reproductive success $R_i(m_1,m_2)$ measures how player i with stimuli m_i fares when encountering another player $j\,(\neq i)$ with stimuli m_j. One can describe Γ also by $\Gamma = (M; R_1(m_1,m_2))$ due to

Lemma 6: *Γ is symmetric, i.e. $R_1(m_1,m_2) = R_2(m_2,m_1)$ for all $m_1,m_2 \in M$.*

Proof.
$$\begin{aligned} R_1(m_1,m_2) &= H_1(s_1^*(m_1,m_2), s_2^*(m_1,m_2); \lambda m_1, \lambda m_2) \\ &= H_2(s_2^*(m_1,m_2), s_1^*(m_1,m_2); \lambda m_2, \lambda m_1) \text{ due to II.2} \\ &= H_2(s_1^*(m_2,m_1), s_2^*(m_2,m_1); \lambda m_2, \lambda m_1) \text{ due to Lemma 5} \\ &= R_2(m_2,m_1) \end{aligned}$$
∎

A necessary condition for an interior $m^* \in M$ to be an evolutionarily stable strategy (ESS) of the evolutionary game $\Gamma = (M; R_1(m_1,m_2))$ is condition

(II.5) $\frac{\partial}{\partial m_1} R_1(m^*,m^*) = 0$

where the differentiability of $R_1(\cdot)$ follows from the differentiability of $s_i^*(m_1,m_2)$ according to Lemma 4. If (II.5) does not hold, m^* does not qualify as a local maximum of $R_1(m,m^*)$ over all $m \in M$ so that an m^*-monomorphic population could be successfully invaded. Because of

$$
\begin{aligned}
&\tfrac{\partial}{\partial m_1} R_1(m_1, m_2) \\
&= \tfrac{\partial}{\partial m_1} H_1(s^*(m_1, m_2); \lambda m_1, \lambda m_2) \\
\textbf{(II.6)} \quad &= \tfrac{\partial}{\partial s_1} H_1(s_1^*(m_1, m_2), s_2^*(m_1, m_2); \lambda m_1, \lambda m_2) \tfrac{\partial}{\partial m_1} s_1^*(m_1, m_2) \\
&+ \tfrac{\partial}{\partial s_2} H_1(s_1^*(m_1, m_2), s_2^*(m_1, m_2); \lambda m_1, \lambda m_2) \tfrac{\partial}{\partial m_1} s_2^*(m_1, m_2) \\
&+ \lambda \tfrac{\partial}{\partial m_1} H_1(s^*(m_1, m_2); \lambda m_1, \lambda m_2)
\end{aligned}
$$

condition (II.5) is equivalent to

$$
\begin{aligned}
&\tfrac{\partial}{\partial s_1} H_1(s_1^*(m^*, m^*), s_2^*(m^*, m^*); \lambda m^*, \lambda m^*) \tfrac{\partial}{\partial m_1} s_1^*(m^*, m^*) \\
\textbf{(II.5')} \quad &+ \tfrac{\partial}{\partial s_2} H_1(s_1^*(m^*, m^*), s_2^*(m^*, m^*); \lambda m^*, \lambda m^*) \tfrac{\partial}{\partial m_1} s_2^*(m^*, m^*) \\
&+ \lambda \tfrac{\partial}{\partial m_1} H_1(s^*(m^*, m^*); \lambda m^*, \lambda m^*) = 0.
\end{aligned}
$$

Let us call $m \in M$ critical if condition (II.5') or, more generally, (II.5) holds.

Given $\lambda = 0$, according to the definition (II.4) of $R_1(m_1, m_2)$, player $1'$s own parameter m_1 influences his fitness $R_1(m_1, m_2)$ only indirectly via the solution $s^*(m_1, m_2)$ of the game $G(m_1, m_2)$ determined by m_1 and m_2. This justifies our interpretation that only in case of an evolutionarily stable $m_1^* = 0$ the survival of the fittest results: According to (II.4), if $m_1^* = 0$ maximizes $H_1(s^*(m_1, m_2); \lambda m_1, \lambda m_2)$ this is equivalent to maximizing player $1'$s fitness $R_1(m_1, m_2)$. In the following we want to explore the conditions for the survival of the fittest, i.e. for an ESS $m^* = 0$ based on $\lambda = 0$:

For $m^* = 0$ the equilibrium $s^*(m^*, m^*)$ of $G(m^*, m^*)$ implies

(II.7) $\frac{\partial}{\partial s_1} H_1(s_1^*(0,0), s_2^*(0,0); 0, 0) = 0$

so that (II.5') for $m^* = 0$ and $\lambda = 0$ simply means

(II.8) $\frac{\partial}{\partial s_2} H_1(s_1^*(0,0), s_2^*(0,0); 0, 0) \frac{\partial}{\partial m_1} s_2^*(0,0) = 0.$

Since (II.8) is a necessary condition for $m^* = 0$ to be an equilibrium of Γ, it is also necessary for an ESS $m^* = 0$ of Γ. Thus for $\lambda = 0$ there are two requirements guaranteeing the necessary condition (II.8) for an ESS $m^* = 0$ of Γ, namely

(II.9) $\frac{\partial}{\partial s_2} H_1(s_1^*(0,0), s_2^*(0,0); 0, 0) = 0$

or

(II.10) $\frac{\partial}{\partial m_1} s_2^* (0,0) = 0.$

Equation (II.9) means that player $1'$s reproductive success does not depend on player $2'$s behavior. Typical examples of such situations are social, but non-strategic environments like, for instance, competitive markets where a seller's success does not depend on the behavior of any individual coseller. Condition (II.9) thus confirms our initial claim (I.i) in a general framework.

Similarly, condition (II.10) justifies (I.ii). It says that the other player's behavior is - at least locally - not influenced by own stimuli. More specifically: If m_1 would change and if according to our assumptions player 2 would be aware of it, player 2's equilibrium strategy remains constant.

In previous studies it has been argued (Bester and Güth, forthcoming, Güth and Huck, 1995, Güth, 1995) that condition (II.10), albeit being a result for the case of known stimuli, already sheds light on situations where stimuli are private information. The argument is simply that privately known stimuli should guarantee that own stimuli cannot influence other players' behavior. All that matters for their behavior are their beliefs based on own stimuli and it may well be that a change of one's own stimuli will not question the other's beliefs concerning them.

In our view, such conclusions should be substantiated by an explicit analysis of games in which stimuli are private information (such an analysis has so far only been performed by Güth and Kliemt, 1995, who investigate an extremely simple extensive game). Although a general indirect evolutionary approach to situations with privately known stimuli faces some technical problems (see in section 6 below), the conjecture will be shown to hold for a narrow, but reasonable class of beliefs concerning the other players' stimuli.

For the case of commonly known stimuli and $\lambda = 0$ our results can be summarized by

Theorem 7: *Let $\Gamma = (M; R_1(m_1, m_2))$ be the evolutionary game defined by (II.3) and (II.4) with the help of the solutions $s^*(m_1, m_2)$ of games $G(m_1, m_2)$ with $m_1, m_2 \in M$. For the survival of the fittest, i.e. for $m^* = 0 \in M$ in case of $\lambda = 0$ to be evolutionarily stable, it is necessary that equation (II.9) holds, confirming (I.i), or that condition (II.10) is true what justifies (I.ii).*

Up to now we only investigated the necessary condition for an interior ESS $m^* \in M$. If for an interior $m^* \in M$ one also would have

(II.11) $\frac{\partial^2}{\partial m_1^2} R_1(m_1, m^*) < 0$ for all $m_1 \in M$,

the only best reply to m^* in Γ would be $m_1 = m^*$. Thus (II.5) and (II.11) for $m^* \in M$ are sufficient to prove that $m^* \in M$ is an ESS of Γ (see Hammerstein and Selten, 1994). Whether (II.11) holds for m^* depends, of course, on the mathematical structure of the model under consideration.

3. An example

To illustrate our general results we consider a simple heterogeneous market with complementary products and individual demand functions

(III.1) $x_i(s_1, s_2) = 1 - s_i - \alpha s_j$ for $i, j = 1, 2$ and $i \neq j$.

Here $x_i(s_1, s_2)$ denotes seller i's sales amount and s_1, s_2 their respective sales prices. The parameter $\alpha\,(\geq 0)$ describes how closely sellers 1 and 2 are interrelated, i.e. for $\alpha = 0$ condition (II.9), substantiating our claim (I.i), should hold.

For the payoffs we assume

(III.2) $H_1(s_1, s_2; m_1, m_2) = s_1 x_1(s_1, s_2) - m_1 x_1(s_1, s_2)$.

In case of $m_1 > 0$ one can interpret the term $m_1 x_1(s_1, s_2)$ as expressing player 1's concern about environmental damage caused by his production activities. For $\lambda = 0$ (reproductive) success on the market, however, depends only on the actual profit $s_1 x_1(s_1, s_2)$. This justifies to characterize an evolutionarily stable $m^* = 0$ as the survival of the fittest. We thus have $S \subset \mathbb{R}$ and $M \subset \mathbb{R}$ with $0 \in M$. By assuming that both, S and M, are closed intervals with non-empty interiors the other assumptions of the previous section are satisfied, too. Later we will specify further conditions to guarantee the economic non-negativity constraints.

Disregarding boundary solutions which will anyhow be eliminated by our more specific restrictions for S, M, and α one obtains the solution
$s^*(m_1, m_2) = (s_1^*(m_1, m_2), s_2^*(m_1, m_2))$ given by

(III.3) $s_1^* = s_1^*(m_1, m_2) = \frac{2-\alpha+2m_1-\alpha m_2}{4-\alpha^2}$

(III.4) $s_2^* = s_2^*(m_1, m_2) = \frac{2-\alpha+2m_2-\alpha m_1}{4-\alpha^2}$.

Since

(III.5) $$\begin{aligned} x_1(s_1^*, s_2^*) &= \frac{4-\alpha^2-(1+\alpha)(2-\alpha)-2m_1+\alpha m_2-2\alpha m_2+\alpha^2 m_1}{4-\alpha^2} \\ &= \frac{2-\alpha-\left(2-\alpha^2\right)m_1-\alpha m_2}{4-\alpha^2}, \end{aligned}$$

reproductive success is given by

(III.6) $R_1(m_1, m_2) = \frac{(2-\alpha+2m_1-\alpha m_2)\left(2-\alpha-\left(2-\alpha^2\right)m_1-\alpha m_2\right)}{(4-\alpha^2)^2} - \lambda m_1 \cdot \frac{2-\alpha-\left(2-\alpha^2\right)\cdot m_1-\alpha\cdot m_2}{4-\alpha^2}$,

with $\lambda \in \{0, 1\}$. To guarantee non-negativity of prices and sales amounts we assume

(III.7) $0 \leq \alpha < \frac{1}{2}$

(III.8) $M = \left[-\frac{1}{3}, \frac{1}{3}\right]$,

and

(III.9) $S = \left[0, \frac{2}{3}\right]$,

what completes the description of the example.

Now, we want to derive the necessary conditions (II.9) or (II.10) for the evolutionary stability of $m^* = 0 \in M$. Since for $\lambda = 0$ one has

(III.10) $\frac{\partial}{\partial s_2} H_1(s^*(0,0); 0, 0) = s_1^*(0,0) \frac{\partial}{\partial s_2} x_1(s^*(0,0)) = -\alpha \frac{2-\alpha}{4-\alpha^2} = -\frac{\alpha}{2+\alpha}$,

condition (II.9) requires

(III.11) $\alpha = 0$,

i.e. that the two sellers are actually monopolists serving two isolated markets, as required in our initial claim (I.i). Since

(III.12) $\frac{\partial}{\partial m_1} s_2^*(m_1, m_2) = \frac{-\alpha}{4-\alpha^2}$

for all $m_1, m_2 \in M$, condition (II.10) also implies (III.11). Thus for $m^* = 0 \in M$ to be evolutionarily stable, one needs $\alpha = 0$; i.e. with commonly known stimuli and $\lambda = 0$ the survival of the fittest can only be expected when the two sellers are completely unrelated. Turned differently this means that two related sellers, i.e. with $\alpha > 0$, will not in general neglect the environmental aspects of their production activities, i.e. the evolutionarily stable $m^* \in M$ will usually satisfy $m^* \neq 0$. It depends, of course, on the sign of m^* whether this will actually reduce pollution what according to (III.1) and (III.3) or (III.4) requires $m^* > 0$.

4. Generalizing the case of commonly known stimuli

When $S \subset E^p$ and $M \subset \mathbb{R}^q$ such that S has a non-empty interior and is convex and compact and that M is convex and compact with $0 \in \text{int}(M)$ and when all our other assumptions are generalized to situation with $p > 1$ or $q > 1$ accordingly, the generalization of our results in section 2 is straightforward. For the sake of simplicity this will be done only for the case $\lambda = 0$ when stimuli influence success only indirectly. Let us, as before, denote by $s_i = (s_i^1, ..., s_i^p)$ and $m_i = (m_i^1, ..., m_i^q)$ an arbitrary element of S and M, respectively. Instead of (II.6) in the multi-dimensional framework one has

$$\textbf{(IV.1)} \quad \begin{aligned} &\nabla_1 R_1(m_1, m_2) = \left(\tfrac{\partial}{\partial m_1^1} R_1(m_1, m_2), ..., \tfrac{\partial}{\partial m_1^q} R_1(m_1, m_2)\right) \\ &= \nabla_1 H_1(s^*(m_1, m_2); 0, 0) * \Box_1 s_1^*(m_1, m_2) \\ &+ \nabla_2 H_1(s^*(m_1, m_2); 0, 0) * \Box_1 s_2^*(m_1, m_2) \end{aligned}$$

where

$$\nabla_1 H_1(s^*(m_1, m_2); 0, 0) = \left(\tfrac{\partial}{\partial s_1^1} H_1(s^*(m_1, m_2); 0, 0), ..., \tfrac{\partial}{\partial s_1^p} H_1(s^*(m_1, m_2); 0, 0)\right)$$

$$\nabla_2 H_1(s^*(m_1, m_2); 0, 0) = \left(\tfrac{\partial}{\partial s_2^1} H_1(s^*(m_1, m_2); 0, 0), ..., \tfrac{\partial}{\partial s_2^p} H_1(s^*(m_1, m_2); 0, 0)\right)$$

$$\Box_1 s_1^*(m_1, m_2) = \left(\tfrac{\partial}{\partial m_1^i} (s_1^j)^*(m_1, m_2)\right) \; j = 1, ..., p; i = 1, ..., q$$

$$\Box_1 s_2^*(m_1, m_2) = \left(\tfrac{\partial}{\partial m_1^i} (s_2^j)^*(m_1, m_2)\right) \; j = 1, ..., p; i = 1, ..., q$$

where "$*$" stands for multiplying a $p \times q$ matrix with a p-vector. With the help of this notation the equivalent condition for (II.5') can be written as

$$\textbf{(IV.2)} \quad \begin{aligned} &\nabla_1 H_1(s^*(m_1, m_2); 0, 0) * \Box_1 s_1^*(m_1, m_2) \\ &+ \nabla_2 H_1(s^*(m_1, m_2); 0, 0) * \Box_1 s_2^*(m_1, m_2) = 0. \end{aligned}$$

Like for $q = 1$ evolutionary stability of stimuli $m^* = 0 \in M$ can be interpreted as the survival of the fittest. Since in the equilibrium $s^*(0,0)$ of $G(0,0)$ the condition

(IV.3) $\bigtriangledown_1 H_1 (s^* (0,0) ; 0,0) = 0$

holds, condition (IV.2), when $m^* = 0$, assumes the simpler form

(IV.4) $\bigtriangledown_2 H_1 (s^* (0,0) ; 0,0)^* \square_1 s_2^* (0,0) = 0$

corresponding to equation (II.8) in the one-dimensional situation. Thus a sufficient, but not necessary, condition, corresponding to (II.9), is

(IV.5) $\bigtriangledown_2 H_1 (s^* (0,0) ; 0,0) = 0$ or $\square_1 s_2^* (0,0) = 0$.

As (II.9) condition (IV.5) justifies the claim (I.i), respectively (I.ii), namely, that the survival of the fittest ($m^* = 0 \in M$) can be expected if a player's payoff does not depend on any of the other's choices, respectively if a player's behavior (equilibrium choice) does not depend on any component of the other player's stimuli.

The strategy set S may be the set of mixed strategies for a finite strategic game $\left(\widehat{S}; H_1 (\cdot, \cdot; m_1, m_2)\right)$, i.e. every $s_i \in S$ is a probability distribution over the finite set $\widehat{S}$. One can then refer to refinements like perfect (Selten, 1975) or proper (Myerson, 1978) equilibria which are defined for finite games. Of course, the other assumptions concerning $H_1 (\cdot, \cdot; m_1, m_2)$ have to be satisfied, too, but they do not contradict the interpretation that the games $G (m_1, m_2)$ are the mixed extensions of some finite games.

If one applies our uniqueness assumption to more refined equilibrium notions, provided they are well-defined and exist, all our analysis remains valid. A careful examination even reveals that the uniqueness assumption may be relaxed in the following way:

There exists a single-valued selection $\varphi : M \times M \to S \times S$ associating an equilibrium solution $\varphi (m_1, m_2) = (\varphi_1 (m_1, m_2), \varphi_2 (m_1, m_2))$ with each game $G (m_1, m_2)$ which is twice continuously differentiable and satisfies the symmetry requirement $(\varphi_1 (m_1, m_2), \varphi_2 (m_1, m_2)) = (\varphi_2 (m_2, m_1), \varphi_1 (m_2, m_1))$.

In spite of the general problems with continuous equilibrium selection (see Harsanyi and Selten, 1988) the differentiability assumption may appear reasonable when considering certain families of games $G (m_1, m_2)$. Of course, $\varphi (\cdot)$ may also select more refined equilibria when these are defined. The game $G (m_1, m_2)$ may also be seen as the normal form of an extensive game $g(m_1, m_2)$. In such a case the selection $\varphi(m_1, m_2)$ may depend on the original extensive game $g(m_1, m_2)$, e.g. $\varphi(m_1, m_2)$ may select the unique subgame perfect equilibrium (Selten, 1965) of $g(m_1, m_2)$. However, one has to assume that all the properties of the selection $\varphi(\cdot)$ are satisfied.

When studying sequential games a typical problem is the non-existence of evolutionarily stable strategies. In such games certain stimuli might guide the behavior in proper subgames which, however, may not be reached at all (see Güth and Kliemt, 1995, for a simple example). Such phenomena typically imply that no evolutionarily stable strategy exists since evolutionary forces cannot drive the evolution of stimuli in unreached information sets.

For the purpose of the study at hand this problem, however, causes no harm since non-existence of ESS typically results from the non-uniqueness of best replies to a supposedly stable $m \in M$. We are not so much concerned with conditions guaranteeing the existence of an ESS or of a coarsening of an ESS (see, for instance, Selten, 1988), but with the necessary condition for $m^* = 0$ to be evolutionarily stable in the sense of (II.8) or (IV.4). Any coarsening of the ESS-concept will also have to satisfy these conditions so that our results will be true regardless of whether the ESS-concept or one of its coarsenings has to be applied.

5. Bayesian equilibria when stimuli are private information

As for the case of commonly known stimuli in Section 2 we focus on one dimensional actions and stimuli, i.e. $S \subset \mathbb{R}$ and $M \subset \mathbb{R}$. More specifically, we consider the class of symmetric Bayesian games

(V.1) $G = (S, M; H_1(s_1, s_2; m_1, m_2); p(\cdot \mid m))$

where $S, M \subset \mathbb{R}$ are closed intervals with non-empty interiors and 0 being an interior value of M. The payoff function $H_1(s_1, s_2; m_1, m_2)$ is assumed to be three times continuously differentiable in all its arguments and satisfies

(V.2) $H_1(s_1, s_2; m_1, m_2) = H_2(s_2, s_1; m_2, m_1)$

for all $s_1, s_2 \in S$ and $m_1, m_2 \in M$. The probability $p_i(\widehat{m} \mid \widetilde{m})$ measures how likely it is for player i's type $\widetilde{m}$ that player $j\,(\neq i)$ is of type $\widehat{m}$. Symmetry of beliefs concerning other's stimuli requires

(V.3) $p_1(\widehat{m} \mid \widetilde{m}) = p(\widehat{m} \mid \widetilde{m}) = p_2(\widehat{m} \mid \widetilde{m})$

for $\widehat{m}, \widetilde{m} \in M$.

A symmetric Bayesian equilibrium of game G is a Borel-measurable function $s^*(\cdot) = s_1^*(\cdot) = s_2^*(\cdot)$ from M to S such that

$$\textbf{(V.4)} \quad \begin{aligned} &\int_M H_1(s^*(m_1), s^*(m_2); m_1, m_2)\, dp(m_2 \mid m_1) \\ \geq &\int_M H_1(s_1, s^*(m_2); m_1, m_2)\, dp(m_2 \mid m_1) \end{aligned}$$

holds for all $s_1 \in S$ and all $m_1 \in M$. When proving the existence of symmetric Bayesian equilibria for games G we rely on type independent or free beliefs $p(\cdot \mid m)$ satisfying

(V.5) $p(\widehat{m} \mid \widetilde{m}) = p(\widehat{m})$ for all $\widehat{m}, \widetilde{m} \in M$.

Further restrictions are that there exists δ such that

(V.6) $\frac{\partial^2}{\partial s_1^2} H_1(s_1, s_2; m_1, m_2) \leq \delta / |M| < 0$ for all $s_1, s_2 \in S; m_1, m_2 \in M$,

where $|M|$ is the length of M. From the continuity of $\frac{\partial^2}{\partial s_1 \partial m_1} H_1(\cdot)$ follows that there exists a positive constant K with

(V.7) $\max\left\{ \left| \frac{\partial^2}{\partial s_1 \partial m_1} H_1(s_1, s_2; m_1, m_2) \right| / \delta \,|\, s_1, s_2 \in S; m_1, m_2 \in M \right\} \leq K / |M|$.

If one only allows for strategies $s(\cdot) : M \to S$ such that

(V.8) $\mid s(\widehat{m}) - s(\widetilde{m}) \mid \leq K \mid \widehat{m} - \widetilde{m} \mid$ for all $\widehat{m}, \widetilde{m} \in M$,

then the set $\mathfrak{S}$ of possible strategies $s(\cdot)$ is convex, uniformly bounded and uniformly continuous. According to Ascoli's Theorem (see, for instance, Arrow and Intriligator, 1981) the set $\mathfrak{S}$ is therefore a compact subset of the set of continuous strategies $s(\cdot)$ in game G.

Theorem 8: *Given the assumptions of games G there exists a symmetric Bayesian equilibrium for all games G if all best replies are interior values of S.*

Proof. We first construct a best reply mapping $\beta(\cdot) : \mathfrak{S} \to \mathfrak{S}$ which is continuous with respect to the maximum norm for continuous strategies $s(\cdot) : M \to S$ and then prove that the requirements of the Brouwer-Schauder-Tychonoff-Theorem are satisfied.

(i) We want to show that for any $s(\cdot) \in \mathfrak{S}$ the best reply $\beta(s)$ is also contained in $\mathfrak{S}$. For all $\widehat{s} \in S$ and $m \in M$ define the expected payoff of the stimuli type m for strategy $\widehat{s}$ by

(V.9) $$F(\widehat{s}, m) = \int_M H_1(\widehat{s}, s(m_2); m, m_2)\, dp(m_2).$$

Because of our assumptions F is three times continuously differentiable in both its arguments. Furthermore,

(V.10) $$\frac{\partial^2}{\partial s_1^2} F(\widehat{s}, m) = \int_M \frac{\partial^2}{\partial s_1^2} H_1(\widehat{s}, s(m_2); m, m_2)\, dp(m_2) \leq \delta < 0,$$

so the best response $\beta(s(\cdot))$ to $s(\cdot)$ is implicitly given by

(V.11) $\frac{\partial}{\partial s_1} F(\beta(m), m) = 0$ for all $m \in M$

due to our assumption that all best replies $\beta(m)$ are interior values of S. By the Implicit Functions Theorem one has

(V.12) $$\frac{d}{dm}\beta(m) = -\frac{\frac{\partial^2}{\partial s_1 \partial m} F(\beta(m), m)}{\frac{\partial^2}{\partial s_1^2} F(\beta(m), m)}.$$

Because of $\mid \frac{\partial^2}{\partial s_1^2} F(\beta(m), m) \mid \geq \mid \delta \mid$ one obtains

(V.13) $$\mid \frac{d}{dm}\beta(m) \mid \leq \frac{1}{|\delta|} \mid \frac{\partial^2}{\partial s_1 \partial m} F(\beta(m), m) \mid \leq K.$$

Hence $\beta(m)$ satisfies condition (V.8), i.e. $\beta(m) \in \mathfrak{S}$. A corollary of part (i) of the proof is that a symmetric Bayesian equilibrium $s(\cdot) \in \mathfrak{S}$ of G is twice continuously differentiable.

(ii) Let us rewrite the function $F(\widehat{s}, m)$, defined in (V.9), as

(V.14) $F(\beta(m), m; s(\cdot)) = \int\limits_M H_1(\beta(m), s(m_2); m, m_2)\, dp(m_2)$

where, as before, $\beta(m)$ is the best reply to $s(\cdot)$ for the m-type of player 1. For any continuous strategy $s(\cdot): M \to S$ let

(V.15) $\| s(\cdot) \| = \max\{| s(m) | : m \in M\}$

be the (maximum) norm of $s(\cdot)$. Let $M(\widehat{s}, \widetilde{s}) = \{m \in M : \widehat{s}(m) \neq \widetilde{s}(m)\}$. Since

$$\begin{aligned}
& | F(\beta(m), m; \widehat{s}(\cdot)) - F(\beta(m), m; \widetilde{s}(\cdot)) | \\
= & \left| \int\limits_{M(\widehat{s}, \widetilde{s})} \tfrac{H_1(\beta(m), \widehat{s}(m_2); m, m_2) - H_1(\beta(m), \widetilde{s}(m_2); m, m_2)}{\widehat{s}(m_2) - \widetilde{s}(m_2)} (\widetilde{s}(m_2) - \widehat{s}(m_2))\, dp(m_2) \right| \\
\leq & \max\left\{ \left| \tfrac{\partial}{\partial s_2} H_1(\beta(m), s_2; m, m_2) \right| : \beta(m), s_2 \in S, m, m_2 \in M \right\} \| \widehat{s}(\cdot) - \widetilde{s}(\cdot) \|
\end{aligned}$$

because of the Mean Value Theorem, the function $F(\beta(m), m; s(\cdot))$, defined in (V.14), is Lipschitz-continuous in $s(\cdot) \in \mathfrak{S}$. Similarly, all its first and second derivatives are Lipschitz-continuous in $s(\cdot) \in \mathfrak{S}$. Because of (V.10) and (V.12) also $\beta(\cdot)$, i.e. the best reply function $\beta(\cdot): M \to S$ against $s(\cdot)$, is Lipschitz-continuous in $s(\cdot)$ and therefore continuous on $\mathfrak{S}$. Thus the existence of a symmetric Bayesian equilibrium $s(\cdot)$ with $\beta(m) = s(m)$ for all $m \in M$ follows from the Brouwer-Schauder-Tychonoff-Theorem (see, for instance, Aliprantis and Border, 1994). ■

6. On the survival of the fittest when stimuli are private information

Let π be the true population distribution over M. As for games with commonly known stimuli we define the evolutionary game by anticipating the solution $s^*(\cdot): M \to S$, i.e. the Bayesian equilibrium derived above. More specifically, let

(VI.1) $G(\pi) = (S, M; H_1(s_1, s_2; m_1, m_2); \pi(\cdot))$

be the Bayesian game with $p(\cdot) \equiv \pi(\cdot)$, i.e. beliefs are determined by the true population distribution. We assume that the (symmetric) Bayesian equilibrium strategy $s^*(\cdot \mid \pi)$ of game $G(\pi)$ for the true distributions $\pi(\cdot)$ over M representing the population composition is unique, i.e. one has $s_i^*(\cdot \mid \pi) = s^*(\cdot \mid \pi)$ for $i = 1, 2$ everywhere. With the help of this notation the evolutionary Bayesian game depends on the true population density $\pi(\cdot)$ over M as follows:

(VI.2) $\Gamma(\pi) = (M; M; R_1(\widehat{m}, \widetilde{m}; m_1, m_2); \pi)$

for all distributions $\pi(\cdot)$ over M, with

(VI.3) $R_1(\widehat{m}, \widetilde{m}; m_1, m_2) = H_1(s^*(\widehat{m} \mid \pi), s^*(\widetilde{m} \mid \pi); \lambda m_1, \lambda m_2)$

In the evolutionary game $\Gamma(\pi)$ the set M of possible stimuli serves both as an action space (players announce stimuli $\widehat{m}$ and $\widetilde{m}$, respectively) and as a type space (players are of certain stimuli types m_1 and m_2, respectively). The true population density $\pi(\cdot)$ determines a player's beliefs concerning the other player's stimuli. As before, λ can assume two values, $\lambda = 0$ and $\lambda = 1$: While in case of $\lambda = 0$ stimuli influence (reproductive) success only indirectly via the solution behavior $s_i^*(m_i \mid \pi)$, in case of $\lambda = 1$ utility equals (reproductive) success.

To allow for polymorphic distributions as stable results of evolutionary processes we rely on

Definition 9: *A distribution $\pi(\cdot)$ over M is evolutionarily stable if $id: M \to M$ with $id(m) = m$ for all $m \in M$ is an evolutionarily stable strategy of $\Gamma(\pi)$.*

For $\lambda = 1$, where utility maximization corresponds to maximizing fitness, we obtain

Proposition 10: *If $\lambda = 1$, then id satisfies the first order condition for an evolutionarily stable strategy of $\Gamma(\pi)$.*

Proposition 10 is a special case of the revelation principle (Myerson, 1979) so that a proof is not needed.

For $\lambda = 0$ the necessary condition is

(VI.4) $\int\limits_M \frac{\partial}{\partial s_1} H_1(s^*(m_1 \mid \pi), s^*(m_2 \mid \pi); 0, 0) \frac{d}{dm_1} s^*(m_1 \mid \pi)\, d\pi(m_2) = 0$

for all $m_1 \in M$. So we can use the one point solution $m_1^* = 0 \in M$, what confirms our initial claim (I.ii) that in case of privately known stimuli, in the sense defined above, only the fittest will survive, i.e. for $\lambda = 0$ only the stimuli $m^* = 0$. Our results are summarized by

Theorem 11: *If stimuli are private information and cannot be signaled at all, evolutionary stability in the sense of the survival of the fittest for $\lambda = 1$ follows from (VI.3) and from (VI.4) for $\lambda = 0$.*

7. The example with stimuli being private information

The necessary condition for maximizing

$$\textbf{(VII.1)} \quad \int_M \left[(s_1 - \lambda m_1)\, x_1(s_1, s_2(m_2))\, d\pi(m_2)\right]$$

is

$$\textbf{(VII.2)} \quad \int_M x_1(s_1, s_2(m_2))\, d\pi(m_2) = \int_M (\lambda m_1 - s_1)\, \tfrac{\partial}{\partial s_1} x_1(s_1, s_2(m_2))\, d\pi(m_2).$$

Thus a symmetric Bayesian equilibrium requires

$$\textbf{(VII.3)} \quad \int_M (1 - s^*(m) - \alpha s^*(\widetilde{m}))\, d\pi(\widetilde{m}) = s^*(m) - \lambda m$$

what implies $s^*(m) = \frac{\lambda}{2} m + \gamma$ for some constant γ and thus

$$\textbf{(VIII.4)} \quad s^*(m) = \tfrac{\lambda}{2} m + \tfrac{1}{3} - \tfrac{\lambda}{6} \mu\pi$$

where $\mu\pi$ is the mean value of m with respect to the distribution $\pi(\cdot)$. According to Proposition 10 any distribution $\pi(\cdot)$ over M is evolutionarily stable for $\lambda = 1$ so that no condition has to be imposed. For $\lambda = 0$ equation (VII.4) implies that

$$\textbf{(VII.5)} \quad \tfrac{\partial}{\partial m} s^*(m) = 0.$$

Thus a change of one's own stimuli neither influences the other's nor the own behavior. For $\lambda = 0$ only $m^* = 0$ can be evolutionarily stable, since maximizing $R_1(\cdot)$ is equivalent to maximizing $H_1(\cdot)$ only if $m = 0$.

8. Conclusions

According to traditional evolutionary analysis (see Hammerstein and Selten, 1994) behavior evolves such that it is optimally adjusted to the population behavior. This has been usually described as the survival of the fittest. It follows from the definition of evolutionary stability, e.g. in the sense of evolutionarily stable strategies which are best replies to themselves.

In an indirect evolutionary analysis one does not study directly the evolution of behavior, but of its underlying stimuli. To determine how behavior depends on stimuli we have applied game theory. Inserting this dependency yields an evolutionary game with stimuli as strategies to which one, as in traditional analysis, can apply concepts of evolutionary stability. We then have asked whether the behavior, implied by the evolutionarily stable stimuli, is optimally adjusted to the population behavior as in traditional evolutionary analysis.

For all situations satisfying our - admittedly - strong differentiability requirements the results confirm the intuition suggested by previous applications: If stimuli are common knowledge, the fittest behavior survives only when own success does not depend on other's behavior or when other's behavior does not react to own stimuli. In case of privately known stimuli results depend on whether stimuli are directly ($\lambda = 1$) or only indirectly ($\lambda = 0$) related to success as described by Theorem 11: Only for $\lambda = 1$ survival of fittest is an immediate implication of evolutionary stability as in traditional evolutionary analysis.

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