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# Pharmacology and Therapeutics Education in the European Union Needs Harmonization and Modernization: A Cross-sectional Survey Among 185 Medical Schools in 27 Countries

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Effective teaching in pharmacology and clinical pharmacology and therapeutics (CPT) is necessary to make medical students competent prescribers. However, the current structure, delivery, and assessment of CPT education in the European Union (EU) is unknown. We sent an online questionnaire to teachers with overall responsibility for CPT education in EU medical schools. Questions focused on undergraduate teaching and assessment of CPT, and students' preparedness for prescribing. In all, 185 medical schools (64%) from 27 EU countries responded. Traditional learning methods were mainly used. The majority of respondents did not provide students with the opportunity to practice real-life prescribing and believed that their students were not well prepared for prescribing. There is a marked difference in the quality and quantity of CPT education within and between EU countries, suggesting that there is considerable scope for improvement. A collaborative approach should be adopted to harmonize and modernize the undergraduate CPT education across the EU.

## Study Highlights

### WHAT IS THE CURRENT KNOWLEDGE ON THE TOPIC?

☑ A previous study showed that few teaching hours in European medical schools were devoted to clinical pharmacology and that there is a lack of trained individuals in this area. Additionally, a recent study showed that the prescribing competencies of final-year medical students in Europe were poor, resulting in many potentially harmful prescribing errors.

### WHAT QUESTION DID THIS STUDY ADDRESS?

☑ This international multicenter study investigated the current structure, delivery and assessment of pharmacology and clinical pharmacology and therapeutics (CPT) education in European Union (EU) medical schools.

### WHAT THIS STUDY ADDS TO OUR KNOWLEDGE?

☑ There is marked variation in the quality and quantity of CPT education within and between EU countries. CPT teaching and assessment throughout the EU is mainly based on traditional learning methods. Most medical schools do not provide students with the opportunity to practice real-life prescribing and do not consider their students to be well prepared for prescribing as a junior doctor.

### HOW THIS MIGHT CHANGE CLINICAL PHARMACOLOGY OR TRANSLATIONAL SCIENCE?

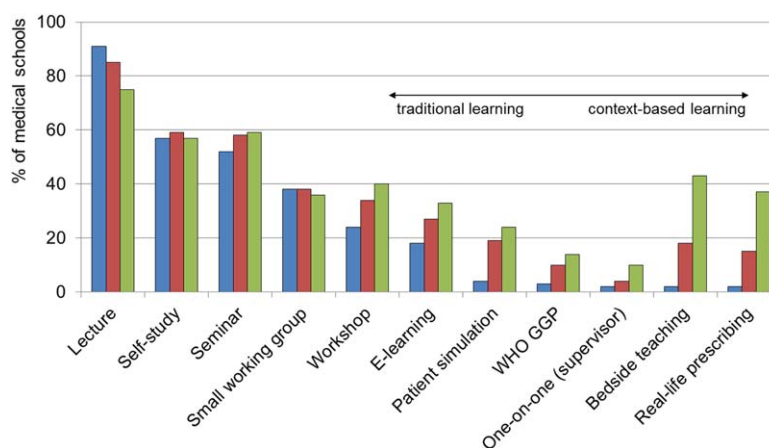
☑ A collaborative approach should be adopted to harmonize and modernize the undergraduate CPT education across the EU.

Prescribing drugs safely and effectively is a fundamental skill that medical graduates must acquire, because after graduation they will prescribe drugs on a daily basis, often with minimal supervision. Inappropriate prescribing may lead to prescribing errors, resulting in exacerbation or prolongation of illness, patient harm, and high healthcare costs.<sup>1,2</sup> Since graduates from medical schools in the European Union (EU) are entitled to work in different EU countries, they should have uniform and adequate prescribing

competencies (i.e., knowledge, skills, attitudes). However, concerns have been expressed that medical graduates across the EU are not adequately prepared for their prescribing duties.<sup>3</sup> In the UK, recently graduated doctors were found to be responsible for a large number of prescribing errors and reported not feeling adequately prepared for their prescribing responsibilities.<sup>4,5</sup> Furthermore, a recent multicenter study involving 17 European medical schools showed a general lack of essential prescribing

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**Figure 2** Traditional learning methods are on the left and context-based learning methods on the right. WHO GGP, World Health Organization Guide to Good Prescribing.<sup>19</sup> Real-life prescribing: the opportunity to prescribe drugs for real patients under the supervision of a senior clinician during clinics. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

The duration of the undergraduate medical curriculum (pre-clinical and clinical years) ranged from 5 to 6 years. In total, 145 of the medical schools (78%) offered a compulsory course in CPT, 21 (12%) an elective course, and 19 (10%) offered no course. Of those schools with a CPT course, 73 (44%) identified their course as vertically, 70 (42%) as spirally, and 23 (14%) as horizontally integrated (see definitions in **Supplementary Material Figure 1**). In all, 176 schools (95%) had a teacher responsible for CPT. The median number of estimated contact hours devoted to CPT teaching during the undergraduate curriculum was 68 (interquartile range 35–100). Countries in the eastern and southern region of the EU used more traditional learning methods, whereas countries in the western and northern region used more problem-based learning methods (**Figure 1**). Basic pharmacology was primarily taught and assessed in the early years of the medical curriculum, whereas clinical pharmacology and therapeutics was taught in the later years (**Supplementary Material Figure 2**).

### Teaching methods and study materials

A variety of teaching methods were used (**Figure 2**). Lectures (75% (basic pharmacology) to 91% (therapeutics)) and self-study (57–59%) were the most common teaching methods for CPT, whereas patient simulation (4–24%) and one-on-one teaching with a supervisor (2–10%) were the least common methods. Some medical schools used bedside teaching (43%) and prescribing in clinics (37%) to teach therapeutics. Lectures (89%) and clinical cases (81%) were the most common study materials for CPT education, whereas eBooks (19%) and mobile applications (13%) were the least common materials (**Figure 3**).

### Teachers involved in teaching development and delivery

In most medical schools, clinical pharmacologists (90%), senior clinicians who were not clinical pharmacologists (77%), and basic pharmacologists (74%) developed and delivered CPT education (**Supplementary Material Figure 3**). Some schools involved pharmacists (42%) and junior doctors (36%), and few involved

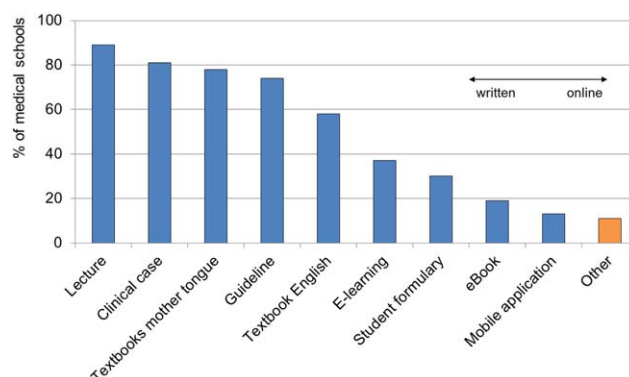
educational experts (21%) or medical/pharmacy students (8%) in the development and delivery of their teaching program.

### Real-life prescribing in clinics

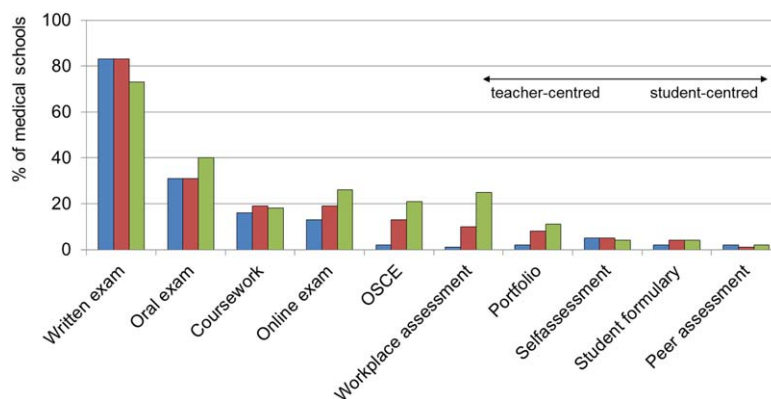
In most medical schools, students did not get the opportunity to practice real-life prescribing for patients under the supervision of a senior clinician on the hospital ward (55%), outpatient clinic (65%), or general practitioner's office (55%). Moreover, many respondents did not know whether students had the opportunity to practice real-life prescribing on the hospital ward (17%), outpatient clinic (20%), or general practitioner's office (22%).

### Assessment methods

A variety of summative assessment methods were used (**Figure 4**). Written (73% (basic pharmacology) to 83% (therapeutics)) and oral examinations (31–40%) were the most common assessment methods for CPT, whereas student formulary (2–4%) and peer assessment (1–2%) were the least common methods. Few medical schools ( $\leq 30\%$ ) used practical assessments, such as objective structured clinical examinations (OSCEs) or workplace assessments in



**Figure 3** Written materials are on the left and online learning resources on the right. Student formulary: specified list of commonly prescribed drugs that students develop during their medical education. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**Figure 4** The teacher-centered methods are on the left and student-centered methods on the right. OSCE, objective structured clinical examination. Workplace assessment: assessing rational prescribing for real patients during clinics. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

clinics. Most schools did not explicitly assess students' dosing knowledge (65%) or drug calculating skills (62%). In contrast to basic pharmacology (33%), most schools integrated the assessment of clinical pharmacology (58%) and therapeutics (64%) into a broader course assessment.

#### Final prescribing assessment

Eighty-six medical schools (47%) had no final prescribing assessment to evaluate final-year students' competencies before graduation, 42 (23%) participated in a national assessment, 34 (18%) had a local assessment ranging from written, oral to online examinations, and 23 (12%) had both.

In the UK, a 2-h national online examination (60 multiple-choice questions (MCQ), extended matching questions (EMQs), prescribing requests) is used to assess prescribing knowledge and skills, such as writing prescriptions, reviewing medication, and calculating drug doses.<sup>10</sup> In the Netherlands, a 2-h national online examination (60 MCQs) focused on ready knowledge required for safe prescribing is used.<sup>11</sup> In both countries, individual medical schools can decide whether this examination is summative or formative. In France, prescribing knowledge is assessed as part of a 2.5-day summative final state examination. This computer-based examination uses narrative patient scenarios (24 cases) combined with MCQs, EMQs, and short answer questions, some of which relate to CPT.<sup>12</sup> In Germany, there is a final state examination involving oral and practical examinations during which CPT can be assessed but is not obligatory. In Slovakia, there is a similar examination but CPT assessment is obligatory. The remaining countries have no final prescribing assessment before graduation, although in Cyprus, Poland, and Italy therapeutic decision-making is evaluated during a compulsory preregistration period after graduation.

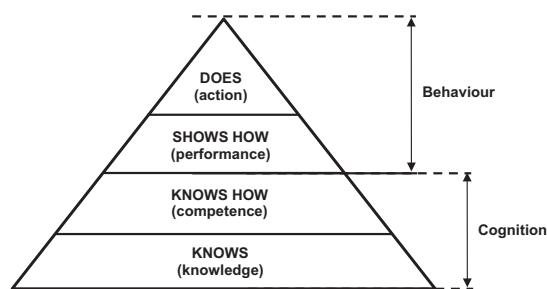
#### Quality, alignment, and structure of learning objectives

In all, 153 medical schools (83%) defined specific learning objectives for CPT during the undergraduate curriculum, and 63 (41%) submitted their objectives for further evaluation. The mean overall quality of the objectives was 1.94 (standard deviation (SD) 0.57), with a score of 1.71 (0.73) for "Specific," 1.89 (0.75) for

"Measurable," 1.98 (0.67) for "Achievable," 1.94 (0.72) for "Relevant," and 2.18 (0.90) for "Time-bound." The objectives of 34 schools (54%) were not or little aligned with the learning and assessment activities, 19 (30%) were partly aligned, and 10 (16%) were adequately aligned. Most of the objectives for basic and clinical pharmacology (93%) and therapeutics (63%) were defined at the "knows" and "knows how" level of Miller's pyramid; 36% of the objectives for therapeutics were defined at the "shows how" level (Figure 5). The most important themes identified in the learning objectives are summarized in **Supplementary Material Table 2**.

#### Being prepared for prescribing

Fourteen (8%) respondents described their final-year medical students as being "not prepared," 113 (61%) as "fairly well," 54 (29%) as "well prepared," and four (2%) as "extremely well prepared" for prescribing as a junior doctor. A common reason for the lack of preparedness was that the CPT education was too theoretical, with too little emphasis on training real-life prescribing in clinical practice (22 free text comments). The probability of being "well prepared" or "extremely well prepared" rather than the other qualifications of preparedness was significantly associated with the presence rather than the absence of a final prescribing assessment (45% vs. 17%,  $P < 0.0001$ ) and the presence rather than the absence of a competence assessment of dosing knowledge (41% vs. 27%,  $P = 0.048$ ).



**Figure 5** Guide to good prescribing. Miller's pyramid for evaluating the structure of learning objectives.

**Table 1 Scoring rubric for pharmacology and clinical pharmacology and therapeutics learning objectives according to the SMART criteria**

Score <sup>a</sup>	Specific	Measurable	Achievable	Relevant	Time-bound
1 = Poor	<ul style="list-style-type: none"> <li>• Broad, vague and unclear objectives</li> <li>• Not specific to drug groups, themes or core drugs and diseases that students should be familiar with</li> </ul>	<ul style="list-style-type: none"> <li>• Objectives are not clearly measurable and documentable</li> </ul>	<ul style="list-style-type: none"> <li>• Objectives are not or hardly feasible given student's abilities and will likely not be achieved within the designated time frame</li> </ul>	<ul style="list-style-type: none"> <li>• Objectives cover no or little relevant knowledge, skills, and attitudes for CPT</li> </ul>	<ul style="list-style-type: none"> <li>• No or unclear time frame by which the objectives should be accomplished</li> </ul>
2 = Suboptimal	<ul style="list-style-type: none"> <li>• Specific objectives, but does not specify knowledge, skills and attitudes in detail</li> <li>• Specified list of themes/drug groups (e.g. cardiovascular drugs) that students should be familiar with but no list of core drugs and diseases</li> <li>• Uses verbs like understand, know, learn, list, describe and explain</li> </ul>	<ul style="list-style-type: none"> <li>• Objectives are only partly measurable and documentable</li> </ul>	<ul style="list-style-type: none"> <li>• Objectives are partly feasible given the student's abilities and can only partially be achieved within the designated time frame</li> </ul>	<ul style="list-style-type: none"> <li>• Objectives cover some relevant knowledge, skills, and attitudes for CPT</li> </ul>	<ul style="list-style-type: none"> <li>• A clear time frame of what should be accomplished within the bachelor's or master's degree or undergraduate curriculum</li> </ul>
3 = Adequate	<ul style="list-style-type: none"> <li>• Specific objectives with a detailed description of the required knowledge, skills and attitudes for CPT</li> <li>• Specified list of core drugs and diseases that students should know about</li> <li>• Describes what the student should be able to do in clinical practice</li> <li>• Uses action verbs like prescribe, choose, show, select, review (NOT understand, learn, know)</li> </ul>	<ul style="list-style-type: none"> <li>• Objectives are clearly measurable and documentable</li> </ul>	<ul style="list-style-type: none"> <li>• Objectives are feasible given the student's abilities and can be achieved within the designated time frame</li> </ul>	<ul style="list-style-type: none"> <li>• Objectives cover most of the relevant knowledge, skills, and attitudes for CPT</li> </ul>	<ul style="list-style-type: none"> <li>• A clear time frame of what should be accomplished within a course, module, semester or academic year</li> </ul>

Based on the SMART mnemonic.<sup>27</sup> Adapted from Lockspeiser *et al.*<sup>28</sup> CPT, pharmacology and clinical pharmacology and therapeutics.

<sup>a</sup>Score per criteria ranged from 1 to 3, with no half points. If objectives did not meet the requirement for a particular score, it received the next lower score.

## DISCUSSION

The main findings of this study are that in the EU 1) CPT education varies greatly within and between countries; 2) CPT teaching and assessment are mainly based on traditional learning methods; 3) more than two-thirds of the schools do not provide students with the opportunity to practice real-life prescribing; 4) the assessment of CPT is often integrated into a broader course assessment, and almost half of the schools do not have a final prescribing assessment; 5) most (69%) medical schools do not consider their students to be well prepared for prescribing as a junior doctor; and 6) the overall quality of CPT learning objectives is poor, and objectives are often not consistent with the learning environment and assessment activities. While there was some variation between schools, these results suggest that there is considerable room to improve CPT education in many EU medical schools.

“Improving and harmonizing the teaching of the rational use of drugs at both undergraduate and postgraduate levels” in Europe is a main goal of the EACPT.<sup>13</sup> It is important to ensure a uniform standard of prescribing among medical graduates, so as to facilitate their mobility across countries. However, we found a marked variation in the quality and quantity of CPT education within and between EU countries. Since the last analysis in 1988 showed similar results,<sup>7</sup> it is surprising that the situation has not improved significantly. However, despite these large differences, some progress has been made in the past three decades. First, several schools have introduced a distinct or integrated prescribing assessment before graduation, and having such an assessment was significantly associated with a better perceived preparedness for prescribing as a junior doctor. A separate and robust prescribing assessment is necessary to ensure that new doctors are able to prescribe safely and effectively,<sup>10</sup> particularly since most schools

**Table 2 Recommendations to harmonize and modernize pharmacology and clinical pharmacology and therapeutics education in the curricula of medical schools in the European Union**

1. CPT should be a clear and visible program throughout the entire medical curriculum, starting as early as possible, and should be emphasized in all clinical modules and attachments.<sup>21,30</sup>
2. Prescribing should be trained in simulated and clinical environments, with emphasis on completing drug prescriptions, reviewing medication charts, and real responsibility for patient care.<sup>16,21</sup>
3. Schools should formulate clear and specific learning objectives, preferably using a detailed list of core drugs ('student formulary') and diseases that students should be familiar with before graduation.<sup>21,30</sup>
4. Schools should ensure that learning objectives are compatible with the learning environment and assessment activities.
5. The WHO 'Guide to Good Prescribing' should be used more intensively in order to teach and train rational prescribing.<sup>17-19</sup>
6. Schools should utilize more online learning resources and preferably share these at national or international level.<sup>20</sup>
7. Medical/pharmacy students and junior doctors should be engaged in 'near peer' education, supervised and trained by clinical pharmacologists and senior clinicians.<sup>22</sup>
8. Clinical pharmacists and nurse prescribers should be given a greater role in the development and delivery of CPT education.<sup>23,24</sup>
9. Schools should implement a robust and separate CPT assessment structure throughout the curriculum, with no compensatory mechanism.<sup>21</sup>
10. Schools should implement a valid and reliable final prescribing assessment at or near the end of the medical curriculum to assess whether graduates are able to prescribe safely and effectively.<sup>10,11</sup>
11. Prescribing should be assessed in a simulated or clinical context, with emphasis on writing prescriptions, verifying the suitability of the treatment choice, giving information to patients, and drug monitoring.<sup>21,30</sup>

Corresponding references are given; CPT, pharmacology and clinical pharmacology and therapeutics.

integrated the assessment of CPT into a broader course assessment, and hence students can compensate for a poor performance in this area by a good performance in other areas. Although the development of final prescribing assessments is promising, future studies should investigate whether these actually improve prescribing objectives after graduation.

Second, more medical schools had an identifiable CPT course (90% in 2016 vs. 77% in 1988), and, on average, more contact hours per school were devoted to CPT education during the undergraduate curriculum (95 h in 2016 vs. 35 h in 1988). Although these findings are encouraging, relatively few hours are devoted to CPT education ( $\pm 2-3\%$  of total study load) compared with other, mainly diagnostic, subjects. Curriculum designers tend to place more emphasis on diagnostic rather than therapeutic reasoning, with the former being perceived as more challenging and difficult.<sup>14</sup> Consistent with the views of final-year students in Europe,<sup>6</sup> CPT education was mainly based on traditional learning methods such as lectures and written examinations, rather than on context-based learning methods, such as patient simulation and workplace assessments. In fact, a large proportion (39%) of schools used solely traditional learning methods, which could in part explain why respondents indicated that students were not well prepared for rational prescribing. The predominance of traditional learning methods in pharmacology education has also been reported in the USA.<sup>15</sup> Rational prescribing is a complex skill that requires various high-level cognitive processes,<sup>16</sup> and thus attending lectures and passing written examinations probably do not prepare students sufficiently for this task. A recent study showed that students taught with mainly traditional learning curricula have significantly weaker prescribing competencies than students taught with mainly problem-based learning curricula.<sup>6</sup> The WHO Guide to Good Prescribing

model has been shown to be the only effective method to teach rational prescribing in a wide variety of international settings,<sup>17-19</sup> yet fewer than 20% of the respondents used this model in their teaching program. This could be because these medical schools provide little practical teaching in the form of role-playing sessions and patient simulation, for which this model is best suited. Although a transition towards more practical teaching is necessary, the resource-intensive format of this teaching could be a challenge for medical schools with a small group of CPT teachers. The traditional aspect of CPT education is also reflected by the extensive use of written materials compared with online learning resources such as E-learning, eBooks, and mobile applications. More medical schools should use and share these online resources because they increase accessibility to information, facilitate personalized training, standardization of content, and are suitable for assessing large cohorts of students simultaneously.<sup>20</sup>

Third, more schools had a designated teacher responsible for CPT education (95% in 2016 vs. 79% in 1988), often a clinical pharmacologist or senior clinician. Such an individual is indispensable for ensuring that the principles of safe and effective use of medicines are emphasized throughout the curriculum.<sup>21</sup> Only a minority of schools actively involved junior doctors and medical/pharmacy students in teaching and education. Yet "near-peer" education has proven to be beneficial and able to reduce the workload of the usually small group of teachers.<sup>22</sup> Clinical pharmacists and nurse prescribers should be given a larger role as educators since they offer additional skills and attributes (e.g., reviewing medication charts) and could improve interdisciplinary collaboration for the prevention of prescribing errors.<sup>23,24</sup>

The quality of CPT learning objectives was generally poor, with objectives often being broad, vague, and incomplete. Only

13 schools used a specified list of core drugs and diseases that students should be familiar with before graduation. Clear objectives are important to verify whether learning outcomes are achieved.<sup>21</sup> Therapeutic objectives were often focused on skills acquisition (e.g., rational prescribing, see **Supplementary Material Table 2**) but did not dovetail with the learning environment (e.g., lectures) and assessment activities (e.g., written examinations). Better coordination between learning objectives and curriculum content is necessary to help students achieve high-level outcomes.<sup>25</sup>

Our results should be interpreted in the light of some limitations. First, data were mainly derived from a single teacher at each school and may have been biased either because the respondents had vested interests or interpreted the questions differently. Second, although definitions were given, there may have been some overlap between CPT themes in the questionnaire. Third, since the questionnaire was not anonymous, respondents may have given socially desirable answers. Fourth, the low response rate in some countries (i.e., Austria, Belgium, Hungary, Italy) might have influenced the results. Fifth, the participating medical schools might have a high standard of CPT education, and thus the results might be optimistic. Sixth, we relied on medical schools to self-report their education, which may not reflect the actual content of the medical curriculum. Seventh, students might be offered other learning activities, which are outside the remit of the responsible teachers and thus not reported in the questionnaire.

## CONCLUSIONS AND RECOMMENDATIONS

Although some progress has been made in the past three decades, this study showed that there is still marked variation in the quality and quantity of CPT education within and between EU countries. This finding may underlie the general lack of prescribing competencies among European medical graduates. Since graduates from medical schools in the EU can move to different EU countries for their postgraduate training, they should have a uniform level of prescribing competencies. In order to achieve this, a collaborative effort is required to harmonize and modernize the teaching and assessment of the rational use of drugs at an undergraduate level. The EACPT Education Working Group has formulated a list of recommendations that can serve as starting point for a harmonized CPT curriculum for EU medical schools (**Table 2**).

## METHODS

This cross-sectional survey involved medical schools in all 28 EU countries and was carried out in the academic year 2015–2016. Since we focused on CPT education during the entire medical curriculum, we excluded medical schools delivering only a preclinical curriculum (i.e., bachelor's degree). Additionally, we excluded private medical schools because their education is not accessible for all students. A 24-item web-based questionnaire (using surveymonkey.com) was developed, based on comparable studies,<sup>7–9,26</sup> and validated by the Education Working Group of the EACPT during an online modification round (**Supplementary Material Figure 1**). The questionnaire asked specific questions about undergraduate teaching and assessment of basic pharmacology, clinical pharmacology and therapeutics, and the preparedness of students for their future task as prescribers. Basic pharmacology was defined as education about the basic principles of how drugs act in biological

systems including pharmacodynamics (e.g., receptor and other drug targets), pharmacokinetics (e.g., absorption, distribution, metabolism, excretion), and pharmacogenetics; clinical pharmacology as education about the application of pharmacological principles and methods in clinical practice (e.g., rational drug selection, adverse drug reactions, drug interactions, errors, adherence); therapeutics as education about the process of rational prescribing for specific clinical conditions (i.e., how to choose a specific drug for an individual patient). Explanations to the questions were provided where appropriate, with opportunity for free text comments. Minor modifications to the content were made after a pilot study with eight CPT teachers from different EU medical schools. The Dutch Ethics Review Board of Medical Education approved the study (Approved Project no. NVMO-ERB 651). Informed consent was obtained from all participants.

A representative from the EACPT Network of Teachers in Pharmacotherapy (NOTIP) was purposely selected from each country to coordinate the survey in his or her country. NOTIP is a European platform for medical schools and CPT teachers. It supports the development and sharing of teaching materials and participation in joint research projects. Each coordinator collected the email addresses of the teacher(s) responsible for undergraduate CPT education at each medical school. If necessary, the national (clinical) pharmacological societies were asked to supply missing contact details. A web link to the questionnaire was e-mailed to the responsible teacher(s) and e-mail reminders were sent 2 and 4 weeks after the initial message. Participation was voluntary and without compensation; confidentiality was guaranteed. The questionnaire took ~15 min to complete. If more than one teacher per school completed the questionnaire, answers were integrated into a final version by the main researcher (D.B.). Based on the survey data, the research team assessed whether CPT education at each school was based on traditional learning or problem-based learning methods. Traditional learning was defined as >50% of the teaching methods consisted of lectures (formal), self-directed learning (textbooks), oral and written exams and essays; and problem-based learning as >50% of the teaching methods consisted of seminars (interactive), small working groups (case scenarios), role playing and patient simulation including OSCEs, clinics including prescribing for real patients. Subsequently, countries with ≥50% of the schools responding were categorized as “only” (>80%) or “mainly” (50–80%) problem-based learning, or “mainly” (50–80%) or “only” (>80%) traditional learning (**Figure 1**).

After completion of the questionnaire, each school was asked to send the undergraduate learning objectives for CPT. The overall quality of these objectives was assessed by the research team using a scoring rubric adapted from the literature (**Table 1**).<sup>27,28</sup> Also, the alignment with the learning and assessment activities during the curriculum were evaluated (1 = no or little alignment, 2 = some alignment, 3 = adequate alignment) and the general themes were identified (**Appendix Table 2**). Additionally, each objective was categorized into one of the four levels of Miller's pyramid (i.e., “knows,” “knows how,” “shows how,” “does”; **Figure 5**).<sup>29</sup> Completed questionnaires were downloaded in Excel format and analyzed using SPSS v. 22.0 (Chicago, IL). The  $\chi^2$  for independence was used to detect statistically significant relationships between two categorical variables.

Additional Supporting Information may be found in the online version of this article.

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#### CONFLICT OF INTEREST

The authors declared no conflict of interest.

#### AUTHOR CONTRIBUTIONS

D.B., J.T., M.O., L.B., T.C., R.L., R.M., J.C., B.T., S.M., E.J.S., M.R., and M.v.A. wrote the article; D.B., J.T., M.O., L.B., T.C., R.L., R.M., J.C., B.T., S.M., E.J.S., M.R., and M.v.A. designed the research; D.B., J.T., M.O., L.B., T.C., R.L., R.M., J.C., B.T., S.M., E.J.S., M.R., and M.v.A. performed the research; D.B. analyzed the data; D.B. contributed new reagents/analytical tools.

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